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OTTAWA, 1959

OBITUARY

Richard Birnie Miller

1915—1959

Courtesy Heath-King Studios, Edmonton

Doctor Richard Birnie Miller, a Member of the Fisheries Research Board of Canada, died February 23, 1959, at his home in Edmonton, after a prolonged illness.

The son of Judge Moore Armstrong Miller, he was born March 29, 1915, in Weyburn, Saskatchewan, where he received his early education. From Weyburn Collegiate Institute he entered the University of Toronto in 1932. In 1934 he won both the Edward Blake Scholarship in Biology and the James A. Barnes Scholarship in Science, and in 1936 he was awarded the G. A. Cox Gold Medal in Science (Biology). From the University of Toronto he received the degrees of Bachelor of Arts in 1936, Master of Arts in 1937, and Doctor of Philosophy in 1939.

In 1937 he joined the staff of the University of Alberta as a Teaching Fellow in the Department of Zoology. In 1939 he returned to Alberta as Lecturer in the same Department. In 1944 he was made Assistant Professor, in 1947 Associate Professor and in 1952 Professor. From 1952 he served as Chairman of the University's Research Fund Committee and from 1956 he was Head of the Department of Zoology.

Doctor Miller's early scientific interests dealt with bottom fauna of lakes. He was one of the first students at the Ontario Fisheries Research Laboratory's new station in Algonquin Park, and participated widely in the early work done there. For his doctor's thesis, he undertook a detailed study of the ecology of the Chironomidae of Costello Lake.

In Alberta he became interested in the cestode *Triaenophorus*, and in 1940 began to study it at Lesser Slave Lake. There he worked out its life history and taxonomy, and became the recognized authority for this genus in North America. In 1943, when changing conditions made it difficult to market whitefish because some were infected with *Triaenophorus crassus*, he played a major part in organizing the whitefish inspection service for the Federal Department of Fisheries, including much liaison work with United States officials concerned with administration of the Pure Food and Drug Act. He also acted as co-ordinator of Canadian *Triaenophorus* research from 1946 to 1952.

Starting in the early 1940's, Dr Miller became interested in the utilization and production of fish stocks, particularly those of prairie streams and lakes, and contributed substantially to our information about whitefish and cisco and trout population dynamics. He demonstrated the ineffectiveness of certain fish-hatchery practices and the usefulness of others—particularly the stocking of "pot-hole" lakes, and streams of different velocities and "cover", with various species of trout. In 1945 he conducted a biological

survey of Great Bear Lake for the Fisheries Research Board of Canada, part of an extensive reconnaissance of large northern waters made in that year.

In recent years Dr Miller had been occupied in tracking down the factors involved in stream survival of "planted" trout, working mostly in streams of the foothills and Rocky Mountains. By 1957 this work had reached the stage where competition of wild fish had been demonstrated to be a major factor in mortality of planted stock. In 1958 he discovered certain physiological deficiencies of the hatchery-reared stock, and how these could be alleviated by using a qualitatively adequate diet. At the time of his death he was completing the analysis of these results and organizing the 1959 field program—which is to be carried out as planned.

Doctor Miller served on the Prairie Provinces Fisheries Investigation Committee in 1944; he acted as Consultant to Alberta's Department of Lands and Forests from 1942, and in 1950 founded the Alberta Biological Station with their support. He served on the National Research Council's Associate Committee on Research on Aquatic Biology from 1952. He was a founding member of the Canadian Conservation Association and an Associate of the Arctic Institute of North America. He served as President of the Canadian Committee for Freshwater Fisheries Research in 1954 and as Vice-President of The Wildlife Society in 1957. From 1956 he was a member of the National Research Council and in 1957 was appointed to the Fisheries Research Board of Canada. He was posthumously elected a Fellow of The Royal Society of Canada.

Doctor Miller's keen mind, the satisfaction he found in research as an intellectual pursuit, his ingenuity in devising apparatus for use in the field and in the laboratory, his deep interest in fisheries research as a means of ultimately benefitting those who use the resource, his unusual command of English, his wide knowledge of biology, dry humour and unobtrusively strong personality, fitted him to play an outstanding role in the development of fisheries science in Canada. His untimely death at 43 has cut short a brilliant career.

W. A. KENNEDY, *Director*

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April, 1959.

Changes in pH, Carbonate and Lactate of the Blood of Yearling Kamloops Trout, *Salmo gairdneri*, During and Following Severe Muscular Activity[1,2,3]

By Edgar C. Black, Wing-gay Chiu, Francis D. Forbes and Arthur Hanslip

ABSTRACT

Alterations in the blood levels of lactate, carbonate, hydrogen ion and hemoglobin following vigorous muscular exercise were studied in yearling Kamloops trout, *Salmo gairdneri*, over four years.

Lactate increased during exercise and during the first 2 hours of rest, returning to the initial level after 6 to 8 hours. Carbonate increased to a maximum during the first 3 minutes of exercise, then dropped precipitously to a minimum far below the initial level after ½ hour of rest, later rose to near the initial level at the 4th hour of recovery, maintained this until the 12th hour, but it had decreased again at the 24th hour. Hydrogen ion concentration rose sharply during the first 3 minutes of activity, then fell off to a stable level a little above the initial figure until the end of exercise, after which it fell substantially below initial level and had not completely recovered after 24 hours of rest. A marked decrease in swimming rate occurred after 3 minutes exercise, following the initial rise of carbonate and hydrogen ion concentration.

INTRODUCTION

The interrelationships among pH, carbonate, degree of oxygenation of hemoglobin, temperature, etc. were thoroughly investigated for mammalian blood by Henderson (1928) and his many associates. The relationships among lactate, chloride and bicarbonate in mammalian blood have been studied by Johnson *et al.* (1945). Laug (1934) investigated the relationships among lactic acid, carbon dioxide and pH of venous blood during recovery from severe exercise in man. While there is considerable information concerning the relationships between pH and the equilibrium between hemoglobin and oxygen in fish blood (Root, 1931; Root, Irving and Black, 1939; Root and Irving, 1941), information on the effects of severe muscular exercise on the disturbance of acid–base relationships in fish blood is meagre. Von Buddenbrock (1938) observed that the blood in the gills of marine fish which have struggled in captivity remains very dark. He estimated the oxygen combining capacity and found it to be greatly reduced, and at the same time noted that lactic acid was present. Auvergnat and Secondat (1942) found that the pH at rest in carp was 7.33, and immediately after 15 minutes of exercise was 7.25, and that the carbon dioxide level decreased in the same circumstances. Secondat (1950) also noted that the oxygen combining capacity of carp blood was reduced following severe muscular exercise. The Bohr effect, or the effect of acid in reducing the ability of hemoglobin to combine with oxygen has been found to be greater in salmonoids (Ferguson and Black, 1941;

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[2]Contribution from the Department of Physiology and the Institute of Fisheries, The University of British Columbia, Vancouver, B.C., and the Fish and Game Branch of the Department of Recreation and Conservation, Province of British Columbia.
[3]The project was supported by the National Research Council of Canada.

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Irving, Black and Safford, 1941) than in carp (Black, 1940). More lactic acid accumulates in the blood of salmonoids, as a result of severe exercise, than in that of carp (Black, 1956, 1957a,b,c; Secondat and Diaz, 1942; Parker and Black, 1959). Accordingly it is of interest to determine the relationships among lactate, carbonate and pH in fish blood with a marked Bohr effect. These relationships have been investigated in yearling Kamloops trout for one temperature only, and are described in the present paper.

METHODS AND MATERIALS

Yearling Kamloops trout, *Salmo gairdneri,* were used for all experiments. The trout eggs were obtained from Beaver Lake in the Okanagan Valley and reared in the Summerland Trout Hatchery operated by the British Columbia Game Department at Summerland, British Columbia. During the summers of 1954, 1955 and 1957, the experiments were carried out at the Summerland Trout Hatchery. In 1956 the experiments were carried out at the laboratory of the Institute of Fisheries at the University of British Columbia, Vancouver. The fish used in the experiments during 1956 were transported from Summerland.

Methods of exercising the fish and of taking blood samples have already been described (Black, 1955). In brief, the fish were exercised by continuous chasing in a standard hatchery trough. Blood was taken by cardiac puncture while the fish respired in water in the inverted position. A heparinized 2-millilitre Luer syringe, lubricated with paraffin oil, was used to draw the blood. The fish had been fed with liver and salmon or mammalian viscera before the start of the experiments, and were not fed during recovery.

Lactate was determined by the method of Barker and Summerson as described in Hawk, Oser and Summerson (1954, pp. 622–624). pH was determined by the use of a Beckman microelectrode used with a standard Beckman, model G, pH meter. Carbon dioxide was analysed by the method of Scholander and Roughton (1943). The centrifuge used was devised by Dr Sydney Segal. Hemoglobin determinations were made using the acid-hematin method (as given in Hawk, Oser and Summerson, 1954, p. 613).

Time necessary to capture the fish and place it in position to obtain blood averaged 25 seconds, with a standard error of the mean of ± 0.9 seconds (range, 5 to 180 seconds). The average time taken to draw blood from the heart was 76 ± 2.6 seconds (range, 9 to 385 seconds). During 1954 the blood sample was introduced into the pH capilliary directly from the syringe. During the other three years, the blood was expelled into a small vial or watch glass and then drawn up into the microelectrode within 50 seconds from the time the blood was taken from the fish. The blood sample for the carbon dioxide analysis was drawn into the micropipette within 15 seconds from the time the blood was taken from the fish. Samples were then taken for hemoglobin and blood lactate determinations.

During 1954, the blood samples for lactate determination were precipitated in tungstic acid. During 1955, 1956 and 1957, the protein was precipitated by the use of zinc sulphate and barium hydroxide.

No attempt was made to maintain the temperature of the glass electrode at the same temperature as the fish. However, the temperature of the electrode was probably from 2 to 10 centigrade degrees higher than the body temperature of the fish, which was 8–12°C.

RESULTS AND DISCUSSION

Results for the four years are tabulated in Table I. The changes in blood levels of carbon dioxide, lactate and hydrogen ion for the year 1957 are illustrated in Fig. 1 and 2.

HEMOGLOBIN

The average hemoglobin level for all conditions and years ranged from 10.7 to 14.6 grams percent. In general, it would appear that the hemoglobin level may increase with activity or with the condition of recovery from activity. Yet there are so many exceptions to this average increase that there is not an unequivocal answer for the immediate effect of exercise on hemoglobin level. Presumably the explanation for an increase in the hemoglobin level, where it did occur, would be an osmotic shift or shifts within the muscle of such a degree as to reduce the effective circulating blood plasma. Upon complete hydrolysis each molecule of glycogen would yield many molecules of lactic acid which would ionize to hydrogen and lactate ions. The intracellular population of osmotically active particles would increase accordingly. Water would diffuse immediately into the muscle cells from the extracelluar fluid including blood till osmotic equilibria were re-established The circulating blood volume would be reduced, which would thereby result in an apparent increase in the level of the hemoglobin. Dr R. E. Haist (personal communication) has suggested that death in fish following activity may be due to a state of shock brought on by loss of circulating fluid volume.

BLOOD LACTATE

The course of the blood lactate level, as illustrated in Fig. 2 for the Kamloops trout, is typical for other salmonoids (Black 1957a,b,c; Parker and Black, 1959). The average resting value for 1957 was 7.2 ± 1.34 mg% (milligrams percent). This increased to 71.1 ± 8.41 mg% following 15 minutes excercise. There was a further increase in the lactate level during the first 2 hours of the recovery period, followed by a decline to near resting levels which may be reached between the 6th and 8th hour of recovery. The shape of the curve for the alteration in blood lactate following maximal vigorous exercise in Kamloops trout is similar to that reported for man by Bang (1936) and Crescitelli and Taylor (1944), but the time factor is considerably different. In man the blood lactate may increase for 10 minutes and generally returns towards the resting value by the end of 50 to 60 minutes. In fish, however, it continued to increase up to 2 hours and did not return to the resting value for at least 6 hours. The difference between the relatively rapid disappearance from the blood in mammals compared with the slow disappearance in fish is due presumably to the slow rate of lactate diffusion at lower temperatures (Johnson *et al.*, 1945).

TABLE I. Weights, hemoglobin, blood levels of lactate, carbon dioxide and hydrogen ion in yearling Kamloops trout, *Salmo gairdneri*, during severe muscular exercise and recovery up to 24 hours. 1954–1957, 11.5°C. Figures shown (except for pH) are mean values followed by the standard error of the mean; below these the number of specimens is given in brackets. For pH, the mean, number of specimens, and range of values are shown.

Year	Place	Before exercise	After 15 minutes' exercise	AFTER RECOVERY TIME OF						
				1 Hour	2 Hours	4 Hours	6 Hours	8 Hours	12 Hours	24 Hours
Weight in grams										
1954	Summerland	64.7±3.80 (9)	67.0±4.51 (10)	...	61.7±4.43 (3)	...	...	...	...	73.3±4.39 (3)
1955	Summerland	59.9±5.76 (11)	59.0±5.40 (11)	...	50.5±6.55 (4)	56.6±4.06 (5)	50.1±2.55 (7)	37.8±7.66 (4)	...	44.0±6.15 (4)
1956	Vancouver	50.0±4.08 (22)	41.3±2.42 (12)	35.9±2.35 (8)	38.8±5.71 (6)	36.3±3.24 (9)	36.3±3.28 (8)	39.4±2.50 (5)	42.7±2.71 (6)	37.0±2.55 (5)
1957	Summerland	46.3±4.58 (8)	47.9±4.59 (7)	51.0±1.84 (5)	38.7±2.16 (6)	45.3±7.61 (6)	37.0±2.01 (6)	35.8±3.15 (5)	37.3±2.93 (6)	37.7±1.11 (5)
Hemoglobin in grams percent										
1954	Summerland	12.0±0.37 (10)	11.8±0.38 (10)	...	12.8±0.83 (3)	...	...	...	...	11.4±0.72 (3)
1955	Summerland	13.0±0.51 (10)	13.7±0.56 (12)	...	13.9±0.62 (3)	14.6±0.82 (5)	13.5±0.52 (6)	11.5±0.21 (4)	...	13.0±1.02 (4)
1956	Vancouver	11.3±0.45 (20)	12.4±0.57 (11)	12.6±0.85 (7)	12.3±2.37 (7)	12.2±0.73 (9)	10.7±0.48 (8)	13.2±0.58 (6)	11.0±0.64 (6)	11.4±0.98 (5)
1957	Summerland	10.8±0.87 (7)	13.6±0.83 (7)	12.1±0.62 (5)	12.9±0.21 (6)	11.8±0.47 (5)	11.8±0.99 (5)	13.1 (2)	11.2±0.38 (5)	12.2±1.52 (3)
Lactate in milligrams percent										
1954	Summerland	16.3±1.45 (10)	104±4.5 (10)	...	185±24.0 (3)	...	...	...	...	17.5±3.15 (3)
1955	Summerland	9.6±1.91 (11)	101±5.4 (12)	...	154±48.1 (3)	127±2.3 (5)	69.3±11.20 (7)	35.4±8.38 (4)	...	12.6±2.60 (4)
1956	Vancouver	5.0±0.88 (22)	37.7±4.79 (12)	52.5±8.49 (8)	69.0±12.60 (7)	89.3±15.42 (9)	75.5±11.22 (8)	7.8±2.31 (6)	5.8±2.11 (6)	8.8±1.18 (4)
1957	Summerland	7.2±1.34 (8)	71.1±8.41 (7)	87.0±12.09 (5)	118±21.6 (6)	71.2±15.24 (5)	20.1±8.42 (4)	12.9±5.91 (5)	11.8±5.61 (6)	1.1±1.11 (4)

1957	Summerland	7.2±1.34 (8)	71.1±8.41 (7)	87.0±12.09 (5)	118±21.6 (6)	71.2±15.24 (5)	20.1±8.42 (4)	12.9±5.91 (5)	(6)	(4)

Carbon dioxide in volumes percent

1954	Summerland	23.1±1.60 (5)	21.1±0.92 (5)	...	13.8 (2)	...	...	...	...	20.9±1.19 (3)
1955	Summerland	17.0±1.48 (8)	14.8±0.70 (4)	...	11.3±0.94 (4)	14.3±0.80 (5)	19.3±1.81 (5)	19.0±1.33 (4)	...	18.3±0.63 (3)
1956	Vancouver	17.7±2.04 (21)	16.9±0.83 (12)	13.7±0.93 (8)	14.1±0.55 (6)	13.8±0.87 (9)	13.3±0.59 (8)	14.5±0.79 (6)	12.5±0.94 (6)	13.3±1.21 (4)
1957	Summerland	27.4±8.89 (6)	26.0±2.26 (7)	22.0±3.58 (5)	20.9±1.17 (6)	26.8±2.87 (6)	27.2±1.55 (6)	27.8±0.50 (3)	27.5±0.66 (6)	22.8±1.17 (5)

Hydrogen ion, $[H^+]$ x 10^{-8}, in equivalents per litre

1954	Summerland	3.85±0.232 (10)	7.04±0.767 (10)	...	4.89±0.863 (3)	...	...	...	...	3.09±0.041 (3)
1956	Vancouver	5.76±0.397 (17)	6.57±0.459 (10)	4.63±0.514 (8)	5.87±0.383 (7)	7.09±0.418 (9)	5.63±0.417 (8)	6.50±0.499 (6)	5.42±0.660 (6)	4.83±0.693 (5)
1957	Summerland	5.03±0.719 (7)	6.31±0.412 (7)	4.16±0.255 (5)	4.11±0.479 (6)	3.86±0.771 (6)	3.35±0.152 (5)	3.49±0.510 (5)	4.00±0.352 (6)	4.56±0.481 (5)

pH

1954	Summerland	7.42 (10) 7.31–7.58	7.15 (10) 6.87–7.31	...	7.31 (3) 7.18–7.41	...	...	...	...	7.51 (3) 7.50–7.52
1956	Vancouver	7.24 (17) 7.10–7.60	7.18 (10) 7.05–7.33	7.33 (8) 7.20–7.65	7.23 (7) 7.14–7.37	7.15 (9) 7.00–7.24	7.25 (8) 7.12–7.48	7.19 (6) 7.10–7.30	7.27 (6) 7.18–7.50	7.32 (5) 7.22–7.60
1957	Summerland	7.30 (7) 7.10–7.56	7.20 (7) 7.10–7.34	7.38 (5) 7.30–7.44	7.39 (6) 7.24–7.64	7.41 (6) 7.16–7.68	7.48 (5) 7.42–7.52	7.46 (5) 7.30–7.72	7.40 (6) 7.29–7.56	7.34 (5) 7.24–7.54

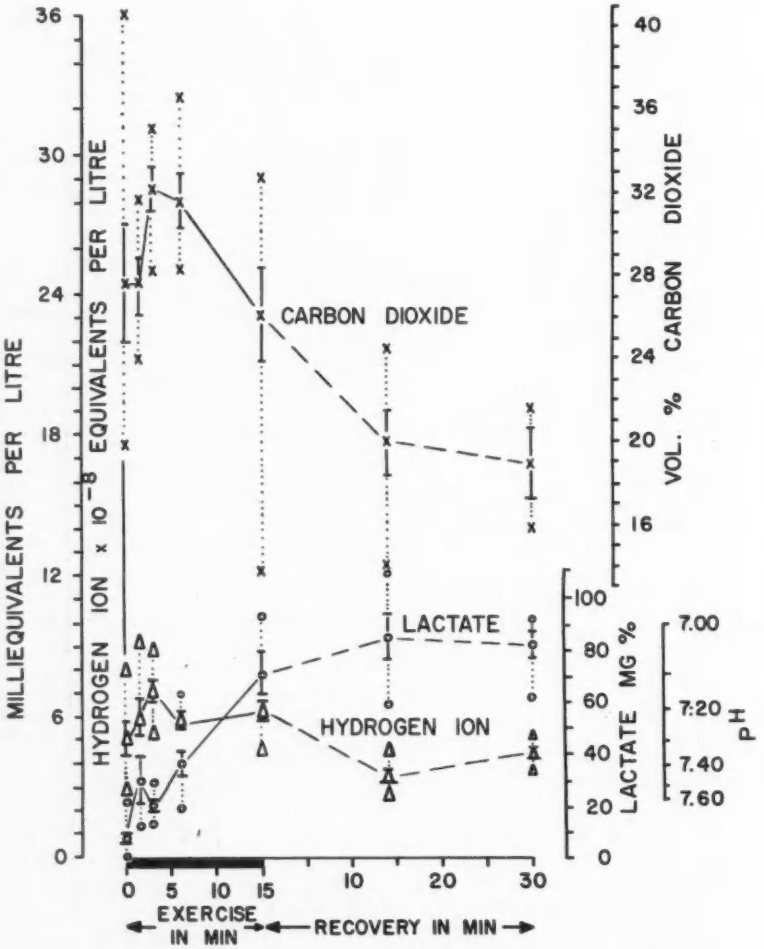

FIG. 1. Changes in blood levels of carbon dioxide, hydrogen ion and lactate in yearling Kamloops trout during 15 minutes of vigorous exercise and 30 minutes post-exercise recovery. 11.5°C, 1957.

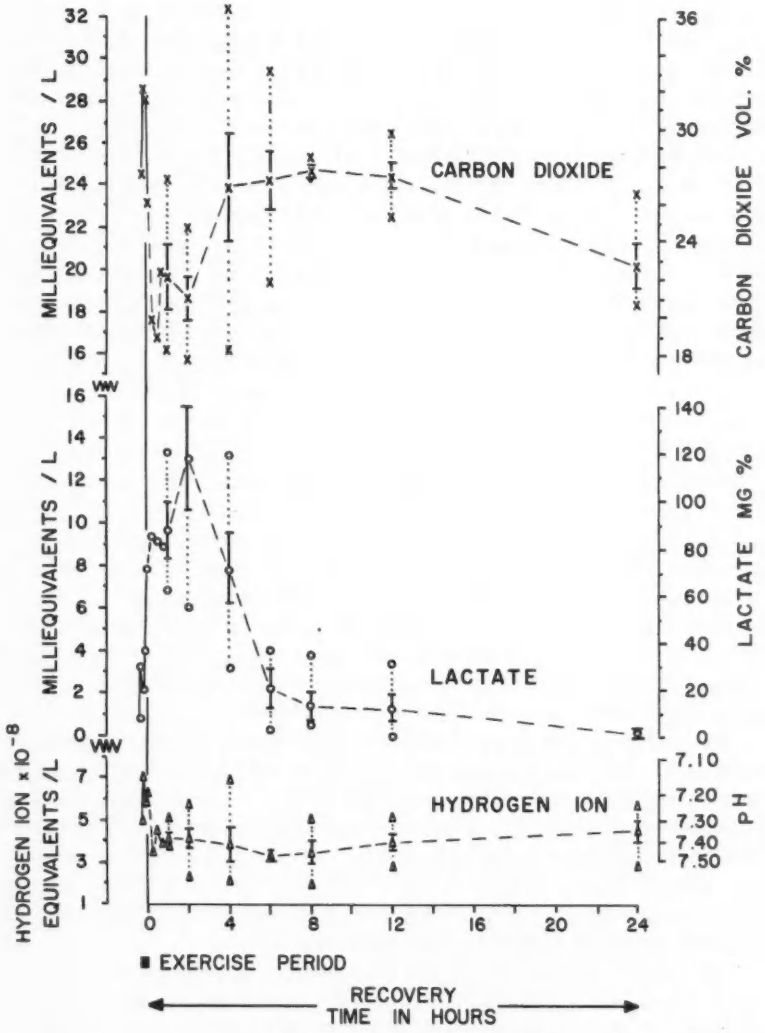

FIG. 2. Changes in blood levels of carbon dioxide, hydrogen ion and lactate in yearling Kamloops trout during 15 minutes of vigorous exercise and 24 hours post-exercise recovery. 11.5°C, 1957.

Some information as to the rate of transfer of lactate from muscle to blood in fishes is to be seen in the work of Leivestad *et al.*, (1957). The experimental conditions of these investigators were very different from those described in this paper. For example, they followed the changes in muscle lactate and blood lactate in marine fishes that had been struggling as a result of exposure to air. Undoubtedly circulation could be arrested as a result of this factor alone, since the mechanics of breathing are interfered with when a fish is exposed to air, and heart action and respiration are closely linked in fishes (Schonlein and Willem, 1895). The probable decrease in circulation in Leivestad's experiments then may greatly affect the transfer of lactate. Taking the results of Leivestad *et al.* as they stand, it would appear that the transfer of lactate from muscle to blood took 4 minutes.

As reported by von Buddenbrock (1938), Secondat and Diaz (1942), Black (1957c) and Parker and Black (1959), not only may fish die as a result of severe muscular exertion, but also a significantly high level of blood lactate is correlated with this mortality. In the experiments in Kamloops trout, however, no mortalities were observed as a result of exercise alone. Mortalities did follow a combination of exercise and cardiac puncture.

Blood Carbonate

Before discussing the work on carbonate, the authors acknowledge that there are two unassessed sources of error in the data presented here. In the first place, the Scholander–Roughton technique was not calibrated against the van Slyke technique. Secondly, the reported carbonate levels may be low due to the possible extraction of carbon dioxide during the taking of the blood samples and the further possible escape of carbon dioxide which could occur during the transfer of blood from the syringe to the micropipette and also from the latter to the Scholander–Roughton syringe. Within these limitations the data may be of value, since differences appeared under different experimental conditions.

The change in the level of carbon dioxide during the first few minutes of exercise is of the greatest importance. As will be noted from Table I and Fig. 1 and 2, the highest levels of carbon dioxide occurred at the end of 3 minutes of activity, then declined to a level that was less than the initial value by the end of the 15 minute exercise period. Thereafter (i.e. during the recovery period), the carbon dioxide fell significantly to the lowest recorded values, which occurred in the first 30 minutes of recovery. However, the levels are still significantly down during the first 2 hours of recovery from vigorous exercise.

The possible explanation for the marked increase in the level of carbon dioxide during the first 3 minutes of activity will be presented below in the discussion of pH changes. A possible reason for the very significant fall in the blood level of carbonate is the transfer of lactate from muscle to blood, since lactic acid is not volatile as is carbonate.

The highest levels of carbonate, accompanied by the least variability appeared at the 8th and 12th hour of recovery.

Auvergnat and Secondat (1942) found that the blood level of carbon dioxide in carp from a level of 35 volumes percent to 17.5 vol % immediately after

15 minutes of strenuous activity. At the 2nd and 6th hours of recovery the values were 16 and 15 vol % respectively.

The fact that the blood carbonate increased strikingly within the first 3 minutes of exercise could account for the marked variations in resting values reported by other workers (for example, Ferguson and Black, 1941, for carp). In other words, any struggling that may have occurred during the sampling procedure may have changed the blood level of carbonate. It is also possible that blood taken from a fish that had struggled, unknown to the experimenter, 1½ to 2 hours previously may have caused a very marked fall in blood carbonate. Such a history would also influence the character of the CO_2-dissociation curve.

Blood pH

The average blood pH for resting fish in the 1957 experiments was 7.30 with a range of 7.10 to 7.56. It will be noted that the lowest values of resting pH overlap with low values found for the exercised condition. There are two explanations for this inconsistency. In the first place, it is probably impossible to obtain a sample of blood from a truly rested unanesthetized fish. On the other hand, the use of anesthetics may alter the normal biochemical equilibria. Secondly, the analytical difficulties and deficiencies already discussed may contribute to the variations encountered.

The changes in hydrogen ion during the first 15 minutes of exercise are illustrated in Fig. 1 for 1957. There was an increase in hydrogen ion concentration during the first 3 minutes of vigorous exercise. This change is associated with a decided and significant reduction in the maximum swimming speed of the yearling Kamloops trout, i.e., of the order of from 16 km/hr (10 mph) to 3.2 km/hr (2 mph) as demonstrated earlier (Black, 1955). Following 3 minutes activity, the hydrogen ion concentration declined somewhat and then continued to decline during the first 15 minutes of recovery. There was a second increase in the hydrogen ion concentration between the 15th and 30th minutes of recovery. Thereafter, the hydrogen ion declined again with the lowest average found at the 6th hour, a time when it also showed the least variation (Fig. 2). Hydrogen ion then increased until, at the end of the 24th hour, the values were not very different from the initial unexercised state.

The first rise in hydrogen ion concentration, during the first 1½ minutes of exercise, is associated with an increase in blood lactate; and the continued rise in hydrogen ion concentration between 1½ and 3 minutes with an increase in the blood level of carbonate and an actual decrease in lactate. This drop in lactate concentration between 1½ to 3 minutes of exercise in these experiments is unexpected and did not appear in the studies reported in 1957 (Black, 1957a). The drop in hydrogen ion concentration through to the first quarter hour of recovery coincides with a marked drop in the blood level of carbon dioxide and a steady rise in the blood lactate level.

It is possible that the initial rise in hydrogen ion concentration and in carbon dioxide level of the blood may be due to an initial transitory increase in hydrogen

ion concentration within the muscle to such an extent as to cause diffusion of hydrogen ion outward as well as to drive carbon dioxide from the intracellular carbonate to the blood. The hydrogen ion may also arise from the initial change of adenosine-triphosphate.The second change in hydrogen ion concentration in the alkaline direction possibly may be due to the diffusion of creatine from the conversion of creatine phosphate to creatine and phosphate. Dubuisson (1939) has shown for frog and turtle smooth muscle that the first increase in hydrogen ion concentration coincides with the initial burst of muscular activity and the conversion of adenosine-triphosphate to adenosine-diphosphate and phosphoric acid. Then the hydrogen ion decreases coincident with the conversion of creatine phosphate to creatine and phosphate compounds which give a relatively alkaline reaction; there is a second increase in hydrogen ion concentration which coincides with the increasing concentration of lactic acid from the release of energy through the breakdown of glycogen. Nakatani (1957) has shown that there is a significant increase in inorganic phosphate, both in blood plasma and in muscle tissue, immediately following 15 minutes of strenuous exercise in adult steelhead trout. Felton (1956) has shown that there is a significant increase in creatine and inorganic phosphate in steelhead trout following 15 minutes of exercise. While the time courses of the changes observed by Nakatani (1957) and Felton (1956) were not reported, it is tempting to suggest that the observations of these workers support the interpretation given above.

Death has been reported following severe muscular activity in chinook salmon fingerlings exercised in fresh water (Anon., 1957), in large 8-pound chinook salmon exercised during trolling (Parker and Black, 1959), and in sockeye salmon raised and exercised in sea water (Black, 1957c). In the work reported by Black (1957c) and Parker and Black (1959), death was associated with a very high level of lactic acid, and occurred in the interval of ½ to 2 hours following exercise in the sockeye salmon and 1½ to 4½ hours in the chinook salmon. While no observations were made on the pH and carbonate levels in these studies, it is possible that death was correlated not only with the high blood level of lactate but also with a low level of carbon dioxide. Death cannot be attributed to a high level of hydrogen ion, on the basis of the experiments presented here. In Fig. 1 and 2, the average hydrogen ion concentration during exercise was not very different from levels reported for the unexercised condition and for 24-hour recovery. On the other hand, some of the lowest ranges of hydrogen ion concentration are seen in Fig. 2 between the 2nd and the 8th hour. From the limited observations made thus far, it is not possible to decide whether or not hydrogen ion may have been at a very high level at the time death occurred in the salmon.

SUMMARY

1. There was no significant alteration in hemoglobin as a result of 15 minutes of strenuous exercise in yearling Kamloops trout.

2. As has been reported earlier, there was a significant increase in the blood level of lactate following 15 minutes of vigorous activity. There was a further

significant increase during the first 2 hours of recovery. The blood levels subsided from this peak to approach resting levels during the first 6 to 8 hours of recovery.

3. There were two alterations in the blood level of carbonate. The carbonate increased during the first 3 minutes of muscular activity to the highest average value encountered. There was a precipitous drop in the blood level of carbonate starting at the 3rd minute of muscular activity and continuing until the 30th minute of recovery. The level then returned upward between the 2nd and 4th hours of recovery.

4. The hydrogen ion concentration increased sharply during the first 3 minutes of activity. Coincident with this increase in hydrogen ion concentration, there was the first increase in lactate and the greatest increase in carbonate resulting from muscular activity. Correlated with these changes there was a very marked reduction in the swimming rate.

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Station List of the 1955-58 Field Investigations of the Arctic Unit of the Fisheries Research Board of Canada[1]

"CALANUS" SERIES NO. 19

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ABSTRACT

A list is given of 180 stations where marine biological, oceanographic and fishing observations or collections were made by the *Calanus* and land-based investigations of the Arctic Unit between Labrador and the Yukon–Alaska boundary from 1955 to 1958.

INTRODUCTION

THREE PREVIOUS STATION LISTS of the *"Calanus"* expeditions (*J. Fish. Res. Bd. Canada*, 9: 65–82, 1952; 11: 98–105, 1954; 13: 41–45, 1956) covered stations occupied between 1947 and 1954. This, the fourth list includes 180 stations occupied by Arctic Unit field investigations between 1955 and 1958, and comprises stations occupied by the *M.V. Calanus* in Labrador, Foxe Basin, northern and eastern Hudson Bay, and by land-based investigations in the Mackenzie District, Banks Island, Coppermine River, Pelly Lake, Frobisher Bay, Baker Lake and the Thelon River system.

To facilitate the finding of stations on the eleven accompanying maps, Table I gives figure numbers for the maps, general locations of the stations on each map, and numbers of the stations found on each map. Further data for individual stations are given in Table II. Areas covered by the maps in Fig. 2–11 are shown in Fig. 1. All the maps were drawn by Miss Berit Arnestad.

TABLE I. Summary of Stations and Maps showing their location

Year	Stations	General location	Figure number
1955	701 to 705	Nain region, Labrador	2
	706 to 714	Northern Hudson Bay and Repulse Bay	5
	715 to 724	Northern Foxe Basin	4
	725 to 731	Northern Hudson Bay	5
	732 to 744	Within 100 miles of mouth of Mackenzie River	11
1956	801 to 839	Northern Foxe Basin	4
	840 to 845	Within 100 miles of mouth of Mackenzie River	11
	846	Between Great Bear and Great Slave Lakes	1
	847 to 849	Pelly Lake	8

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TABLE I: *continued*

Year	Station	General location	Figure number
1957	901	Northern Foxe Basin	4
	902 to 908	Within 15 mile radius of Coppermine	9
	909 to 915	Along Mackenzie River from Aklavik to Fort Norman	11
	916	Frobisher Bay, Baffin Island	3
1958	58–1 to 58–19	Belcher Islands, Hudson Bay	7
	58–20 to 58–21	Northern Hudson Bay	5
	58–22 to 58–33	Eastern Hudson Bay	6
	58–34 to 58–36	Belcher Islands, Hudson Bay	7
	58–37 to 58–38	Eastern Hudson Bay and James Bay	6
	58–39	Northern Ellesmere Island	1
	58–1001 to 58–1009	Head of Frobisher Bay, Baffin Island	3
	58–1010 to 58–1016	Baker Lake and Thelon River System	8
	58–1017 to 58–1021	Anderson River	11
	58–1022 to 58–1027	Banks Island	10
	58–1028 to 58–1029	Horton River	11
	58–1030	Tuktoyaktuk	11

TABLE II. List of Stations, 1955 – 1958.

Station	Map location	North Latitude	West Longitude	Depth (*metres*)	Type of station (work done)
	1955				
701	2 miles northeast of Nain, Labrador	56°34′	61°38′	100–110	plankton, benthos
702	Nain	56°32.5′	61°41.5′	0–7	handline fishing, littoral, benthos, hydrographic
703	Lake about 9 miles west-south-west of Nain	56°30′	61°57′	*ca.* 20	handline fishing, hydrographic
704	Challenger Cove, Labrador	56°43′	61°38′	0–22	benthos, littoral
705	Port Manvers, Labrador	56°57′	61°30′	0	littoral
706	Digges Island, north-east Hudson Bay	62°34′	77°52′	0	littoral
707	East of Mansel Island, Hudson Bay	62°11′	79°12′	36	plankton
708	East of Bencas Island, Hudson Bay	63°01′	82°37′	17	plankton, benthos
709	Northeastern Coats Island, Hudson Bay	63°00′	82°16′	36	plankton

TABLE II: *continued*

Station	Map location	North Latitude	West Longitude	Depth (*metres*)	Type of station (work done)
710	Repulse Bay	66°31′	86°15′	0–3	benthos, littoral
711	"	66°28′	86°12′	70–110	benthos, plankton
712	25 miles northeast of Winter Island, Foxe Basin	66°37′	82°20′	11–14	plankton, benthos
713	5 miles south of Cape Wilson	66°55′	81°20′	25–49	plankton, benthos, hydrographic
714	North of Cape Jermain	67°48′	81°45′	20	plankton
715	Skeoch Bay	69°34′	80°17′	0–15	plankton, benthos, littoral, hydrographic
716	South of Tern Island	69°23′	80°49′	92–110	plankton, benthos, hydrographic
717	East coast of Igloolik Island	69°23.5′	81°29′	14	plankton, hydrographic
718	Hooper Inlet	69°18.5′	81°35.5′	75	plankton, benthos, hydrographic
719	Hooper Inlet	69°20.5′	81°43.5′	51	plankton, benthos, hydrographic, long line fishing
720	Turton Bay	69°21.5′	81°40.5′	0–18	littoral, hydrographic
721	Lake on Igloolik Island	69°23.5′	81°39′	...	gill-net fishing
722	Hooper Inlet	69°20′	82°00′	36–45	plankton, benthos, hydrographic
723	Turton Bay	69°22.7′	81°44.3′	22–24	plankton, benthos, hydrographic
724	Lake 15 miles southwest of Igloolik	69°13′	82°18′	...	gill-net fishing
725	South of Coral Harbour, Southampton Island	63°45′	83°02′	55	plankton, hydrographic
726	"	63°40′	82°40′	58	plankton, hydrographic
727	"	63°50′	83°25′	56	plankton, hydrographic
728	South of Coral Harbour	63°43′	83°37′	40+	plankton, hydrographic
729	"	63°46′	83°30′	52	plankton, hydrographic
730	"	63°47′	83°28′	53	hydrographic
731	"	63°33′	83°23′	70+	plankton
732	Aklavik	68°13′	135°00′	...	fishing
733	Whitefish Station East	69°23′	133°37′	...	fishing, whaling
734	Small lake near Whitefish Station East	69°21′	133°34′	...	fishing, littoral

TABLE II: *continued*

Station	Map location	North Latitude	West Longitude	Depth (*metres*)	Type of station (work done)
735	Tuktoyaktuk	69°27′	132°58′	...	fishing
736	Nicholson Point	69°56′	128°54′	...	fishing, littoral
737	Stanton	69°45′	128°53′	...	fishing, littoral
738	Harbour in Husky Lakes	69°49′	130°19′	...	fishing, littoral
739	Island in Husky Lakes	69°32′	131°19′	8	benthos
740	Finger Inlet in Husky Lakes	69°19′	131°07′	...	fishing
741	Sitidgi Lake	68°40	132°48′	...	fishing
742	Mouth of Sitidgi River	68°42′	132°58′	...	fishing
743	Harbour at south end of Husky Lakes	68°52′	133°28′	...	fishing, littoral
744	Pauline Cove, Herschel Island	69°34′	138°54′	...	fishing, littoral sealing
	1956				
801	½ mile east of Igloolik Point	69°20.5′	81°26′	10	plankton, benthos
802	Turton Bay	69°22.5′	81°46.5′	...	littoral
803	Hooper Inlet	69°20′	81°39′	54	plankton
804	"	69°18.4′	81°34.1′	45–51	plankton, hydrographic
805	Hall Beach	68°46′	81°11′	9	benthos
806	Frustration Bay, Rowley Island	69°06′	79°11′	0–8	plankton, benthos
807	"	69°05.5′	79°11′	...	fishing
808	Gifford Fjord	70°08.4′	82°20′	160–174	plankton, benthos, hydrographic
809	"	70°04.8′	81°58′	...	littoral
810	Fury and Hecla Strait, Augarnar Point to Neerlonakto Island	69°42′	80°59′	39–55	plankton, hydrographic
811	"	69°37.2′	81°06.3′	106	plankton, benthos, hydrographic
812	"	69°32.8′	81°14′	131	plankton, hydrographic
813	"	69°27.6′	81°22.5′	18	hydrographic
814	Fury and Hecla Strait, Bouverie Islands to Sevigny Point	69°40.8′	82°08′	55	hydrographic
815	"	69°43.2′	82°07′	55	hydrographic
816	"	69°46.5′	82°07.5′	55–80	plankton, benthos, hydrographic
817	Skeoch Bay	69°36′	80°13′	19–20	plankton, benthos, hydrographic
818	South of Tern Island	69°24′	80°53′	95	plankton, benthos, hydrographic

TABLE II: *continued*

Station	Map location	North Latitude	West Longitude	Depth (*metres*)	Type of station (work done)
819	Near 810	69°41.3′	80°52′	7	plankton
820	Murray Maxwell Bay	69°55.7′	80°19′	73	plankton, benthos, hydrographic
821	"	70°00.5′	80°12′	0–30	littoral, benthos
822	West of Calthorpe Islands	69°27.2′	80°26.5′	29	benthos
823	Near 822	69°22.2′	80°18.5′	15	benthos
824	Jens Munk Island to Koch Island	69°40.7′	79°13.5′	27	plankton, benthos, hydrographic
825	"	69°37.3′	78°59.5′	85	plankton, hydrographic
826	"	69°32.8′	78°51′	50	plankton, hydrographic
827	Koch Island to Rowley Island	69°23.1′	78°34.9′	27	plankton, hydrographic
828	"	69°25.7′	78°33′	27–33	plankton, benthos, hydrographic
829	"	69°28.1′	78°29.5′	13	plankton, hydrographic
830	Koch Island to Cape Jensen, Baffin Island	69°40.7′	77°51.1′	20	hydrographic
831	"	69°42.2′	77°46′	71	plankton, benthos, hydrographic
832	"	69°44′	77°38.2′	79–90	hydrographic
833	Baffin Island to Turner Point, Bray Island	69°34.8′	77°05.9′	27	plankton, hydrographic
834	"	69°31	77′°07′	18–22	plankton, hydrographic
835	"	69°26.2′	77°08.5′	9	plankton, hydrographic
836	Bray Island to Rowley Island	69°15.7′	77°30.9′	10	plankton, hydrographic
837	"	69°16′	77°48′	45–55	plankton, benthos, hydrographic
838	"	69°17.2′	78°06′	23–27	plankton, hydrographic
839	Turton Bay	69°22.5′	81°47.6′	0–6	littoral
840	Stream 2 miles north of Aklavik	68°15′	135°01′	...	fishing
841	Whitefish Station East	69°23′	133°38′	...	fishing
842	Small lake near Whitefish Station East	69°21′	133°34′	...	fishing, littoral
843	Mouth of Firth River	69°33′	139°21′	...	fishing
844	Pauline Cove, Herschel Island	69°34′	138°54′	...	fishing
845	King Point Harbour	69°06′	137°54′	...	fishing
846	Jackfish Lake	63°43′	117°30′	...	fishing

TABLE II: *continued*

Station	Map location	North Latitude	West Longitude	Depth (*metres*)	Type of station (work done)
847	Near south end of Pelly Lake	65°49′	102°07′	...	fishing, plankton
848	Central region of Pelly Lake	65°55′	101°24′	...	fishing, plankton
849	East End of Pelly Lake	65°53′	100°57′	...	fishing, plankton
	1957				
901	Frustration Bay, Rowley Island	*ca.* 69°06′	*ca.* 79°11′	0–34	plankton, benthos, littoral, hydrographic, fishing
902	John Brown Island, Coppermine River	67°50′	115°02′	...	fishing, littoral
903	Seep on John Brown Island	*ca.* 67°50′	*ca.* 115°02′	...	littoral, plankton
904	About 9 miles up Coppermine River	67°46′	115°19′	...	fishing
905	Small lake about 4 miles up Coppermine River	67°47′	115°10′	...	fishing
906	Seven Mile Island, near Coppermine	67°55′	114°55′	...	fishing, littoral, plankton
907	Mouth of Rae River	67°55′	115°37′	...	fishing, littoral, plankton
908	Mouth of Richardson River	67°50′	115°32′	...	fishing
909	Mouth of Firth River	69°33′	139°21′	...	fishing
910	Aklavik	68°12′	134°59′	...	fishing
911	Fort McPherson	67°26′	134°53′	...	fishing
912	Arctic Red River	67°27′	133°45′	...	fishing
913	Fort Good Hope	66°15′	128°38′	...	fishing
914	Norman Wells	65°17′	126°52′	...	fishing
915	Fort Norman	64°54′	125°36′	...	fishing
916	Ogac Lake, Frobisher Bay	*ca.* 62°51′	*ca.* 67°21′	...	plankton, benthos, hydrographic, fishing
	1958				
58–1	North Omarolluk Sound, Belcher Islands	56°26′	78°53′	21.5	hydrographic
58–2	"	56°24′	78°49′	19.5	plankton, hydrographic
58–3	"	56°25.5′	78°55.5′	6–7	plankton, benthos, metabolism, primary production
58–4	"	56°25.5′	78°54′	21	plankton, benthos, hydrographic, metabolism, primary production

TABLE II: *continued*

Station	Map location	North Latitude	West Longitude	Depth (*metres*)	Type of station (work done)
58–5	"	56°25.5′	78°55.5′	0	littoral, metabolism
58–6	River mouth west of Gushie Point	56°25.5′	79°00′	...	fishing
58–7	Lake southwest of Gushie Point	56°24.7′	79°56′	...	plankton
58–8	North Omarolluk Sound	56°26.2′	78°46.5′	34	plankton, hydrographic
58–8A	"	56°26.5′	78°47.5′	40	plankton, benthos
58–9	South of Spence Harbour	56°15.5′	78°57.3′	19	benthos
58–10	"	56°16′	78°57.5′	10+	primary production
58–11	Spence Harbour	56°17′	78°57.5′	0	littoral, metabolism
58–12	"	56°17′	78°57.5′	shallow	plankton
58–13	North Omarolluk Sound	56°16.5′	78°53.7′	32	plankton, metabolism
58–14	East side of Kipaluk Inlet	56°17′	78°58.4′	0	littoral
58–15	North Omarolluk Sound	56°15.2′	78°56.5′	33	plankton, benthos, hydrographic, metabolism
58–16	"	56°19.8′	78°51′	15	plankton, hydrographic, primary production
58–17	Northeast of LaDuke Island	56°08′	78°58.5′	25	plankton, hydrographic, primary production
58–18	Bloody Island Bay	56°08.5′	78°54.5′	...	metabolism
58–18A	"	56°09.5′	78°53.5′	14	plankton
58–19	Central Omarolluk Sound	56°08.5′	78°59.5′	60–67	plankton, hydrographic
58–20	Digges Island	62°34′	77°52′	13	plankton, benthos, hydrographic, metabolism
58–21	5 miles west of Digges Island	62°36′	78°16′	50–53	plankton, benthos, hydrographic
58–22	Off Kuvik Bay, Hudson Bay	61°34′	78°32′	100	plankton, benthos, hydrographic
58–23	Cape Smith	60°44′	78°26′	7	plankton, benthos, hydrographic
58–24	10 miles west of Cape Smith	60°40′	79°04′	130	plankton, hydrographic
58–25	20 miles west of Cape Smith	60°40′	79°25′	146	hydrographic
58–26	30 miles west of Cape Smith	60°40′	79°45′	165	plankton, benthos, hydrographic

TABLE II: *continued*

Station	Map location	North Latitude	West Longitude	Depth (*metres*)	Type of station (work done)
58–27	Ottawa Islands	59°05′	80°40′	7	plankton, benthos, hydrographic
58–28	Ottawa Islands to Quebec coast	59°04′	80°27′	115	plankton, benthos, hydrographic
58–29	"	59°01′	79°48′	110	hydrographic
58–30	"	58°59′	79°09′	100	plankton, hydrographic
58–31	Port Harrison	58°26.5′	78°10′	20–29	plankton, benthos, hydrographic
58–32	Sleeper Islands	57°31′	79°41′	12	plankton, benthos, hydrographic
58–33	Southeast of Sleeper Islands	57°23′	79°39′	90–95	plankton, benthos, hydrographic
58–34	Trading Post, Belcher Islands	56°12′	78°52.5′	2–0	benthos, fishing
58–35	South Omarolluk Sound	55°46.5′	79°08′	6	plankton, fishing, hydrographic
58–36	South of Innetalling Is.	55°47.5′	79°11′	79–130	plankton, benthos, hydrographic
58–37	South of Belcher Islands	55°15′	79°30′	110–125	plankton, benthos, hydrographic
58–38	Off mouth of Moose River, James Bay	*ca.* 51°22′	*ca.* 80°14′	3	plankton, hydrographic
58–39	Hazen Lake, Baffin Island	*ca.* 81°50′	*ca.* 71°00′	...	plankton, benthos, hydrographic, primary production, fishing
58–1001	Sylvia Grinnell Lake, Baffin Is.	64°10′	69°20′	...	fishing
58–1002	Mouth of Sylvia Grinnell River	63°43′	68°32′	...	fishing
58–1003	Bear Island, Frobisher Bay	63°45′25″	68°29′	70	fishing
58–1004	Small lake about 5 miles from head of Frobisher Bay	63°42′	68°23′	...	fishing
58–1005	Lake at southwest corner of Frobisher Bay	63°44′	69°02′	...	fishing
58–1006	Mouth of Sharat River on south side of Frobisher Bay	63°38′	68°48′	...	fishing, littoral
58–1007	Small lake 6 miles from mouth of Sylvia Grinnell River	63°45′	68°36′	...	hand seine fishing
58–1008	Mouth of Jordan River	63°45′	68°57′	...	fishing, littoral
58–1009	Lake at head of Ward Inlet	63°28′	67°24′	...	fishing

TABLE II: *continued*

Station	Map location	North Latitude	West Longitude	Depth (*metres*)	Type of station (work done)
58–1010	Kikatawa Lake outlet	64°10.5′	96°08′	...	fishing
58–1011	Mouth of Prince River	64°17′	95°44′	...	fishing
58–1012	Mouth of Ann River	64°18′	95°20′	...	fishing
58–1013	Mouth of Thelon River	64°17′	96°05′	...	fishing
58–1014	Schultz Lake	64°45′	97°30′	...	fishing
58–1015	North shore of Aberdeen Lake	64°30′	99°00′	...	fishing
58–1016	Mouth of Dubawnt River	64°32′	100°07′	...	fishing
58–1017	Fork of Anderson River	68°25′	128°50′	...	fishing
58–1018	Anderson River, 120 miles from mouth	68°45′	128°25′	...	fishing
58–1019	Anderson River, 35 miles from mouth	69°22′	128°18′	...	fishing
58–1020	Small lake adjacent to Anderson River	69°22′	128°18′	...	fishing
58–1021	Mouth of Anderson River	69°43′	128°57′	...	fishing
58–1022	Small lake at Sachs Harbour, Banks Island	71°59′	125°14′	...	fishing
58–1023	"	71°56′	124°49′	...	fishing
58–1024	Fish Lake, Banks Island	71°50′	124°38′	...	fishing
58–1025	Lake on Banks Island	72°16′	125°15′	...	fishing
58–1026	Raddi Lake, Banks Island	71°42′	123°42′	...	fishing
58–1027	Lake on Sachs River	71°49′	124°31′	...	fishing
58–1028	Horton River	69°55′	126°46′	...	fishing
58–1029	Lake near Horton River	69°57′	126°57′	...	fishing
58–1030	Tuktoyaktuk	69°27′	133°03′	...	fishing

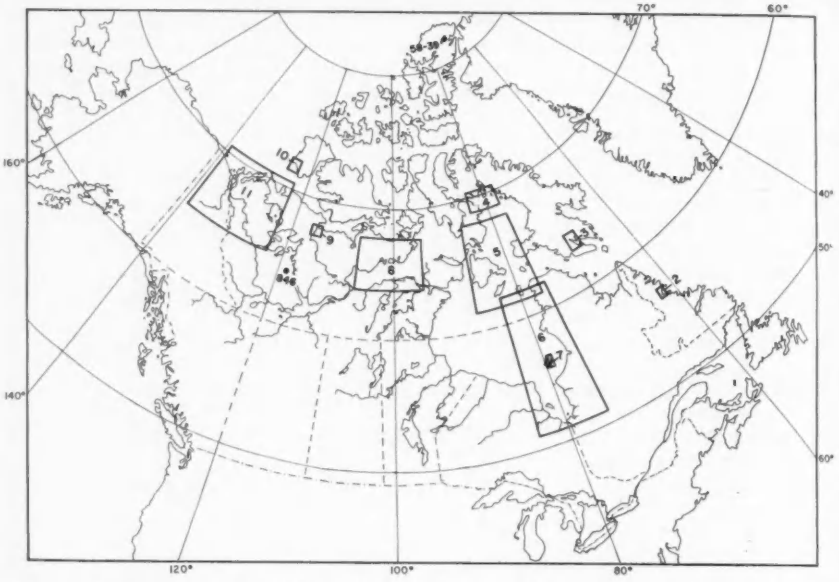

FIG. 1. Canada, showing areas covered by Figures 2 to 11 and stations not on other maps.

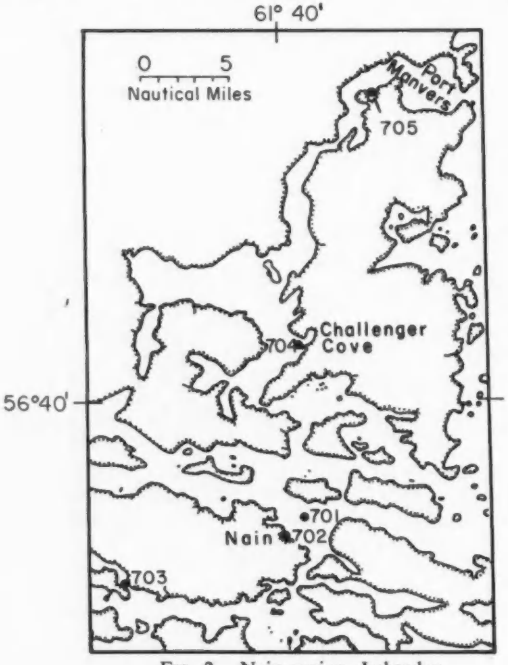

FIG. 2. Nain region, Labrador.

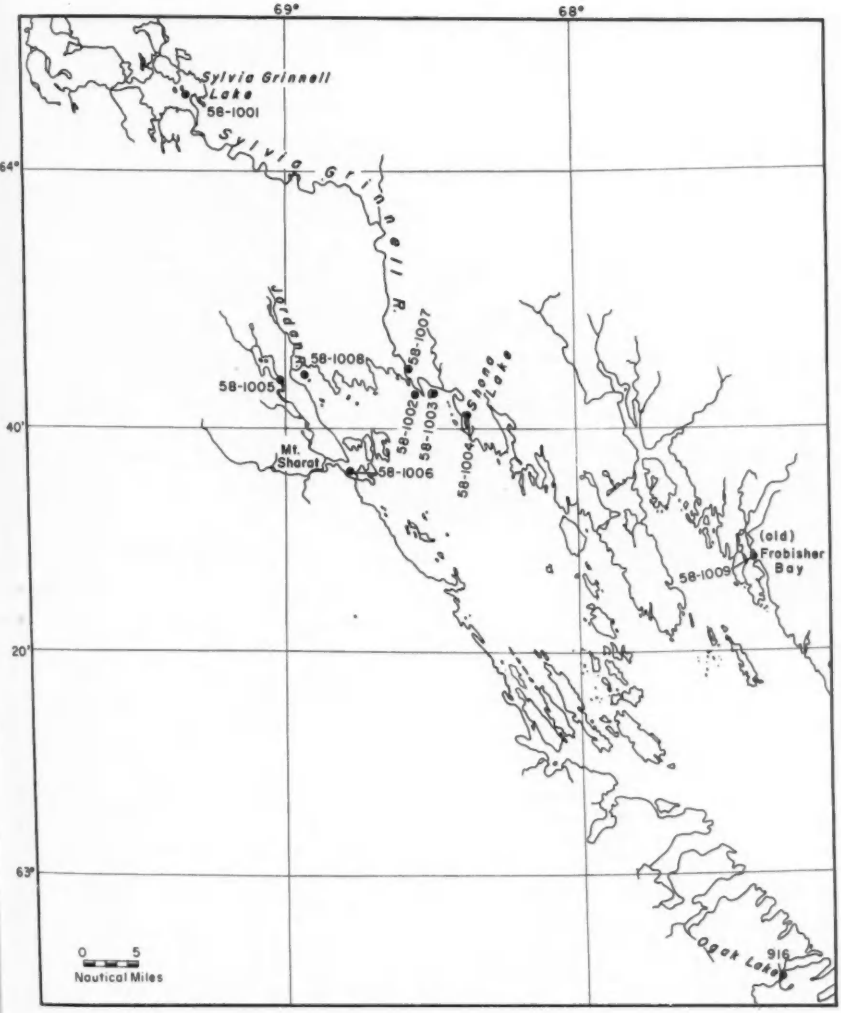

FIG. 3. Head of Frobisher Bay.

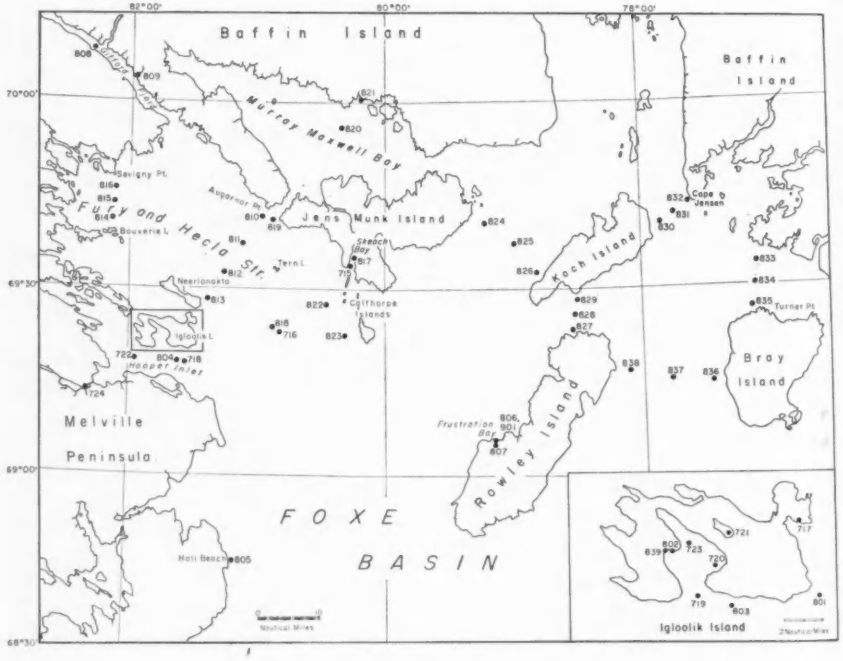

FIG. 4. Northern Foxe Basin.

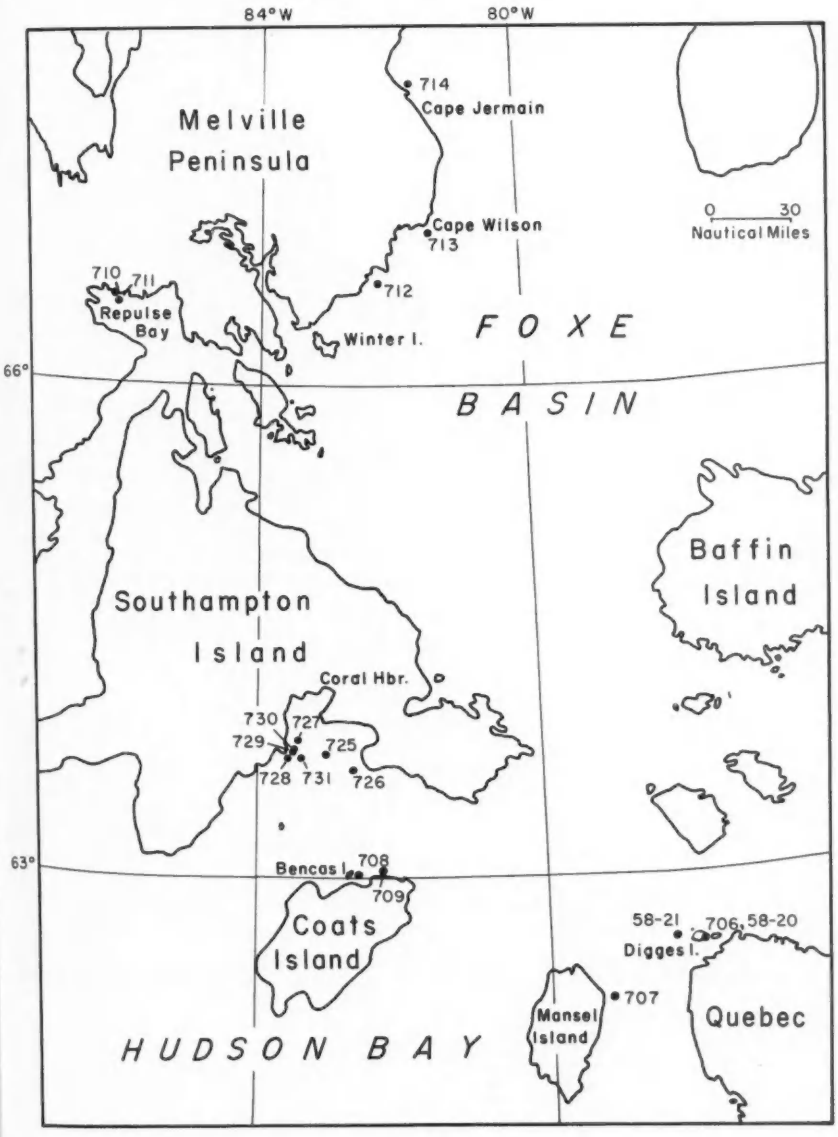

FIG. 5. Northeastern Hudson Bay and Repulse Bay.

FIG. 6. Eastern Hudson Bay and James Bay.

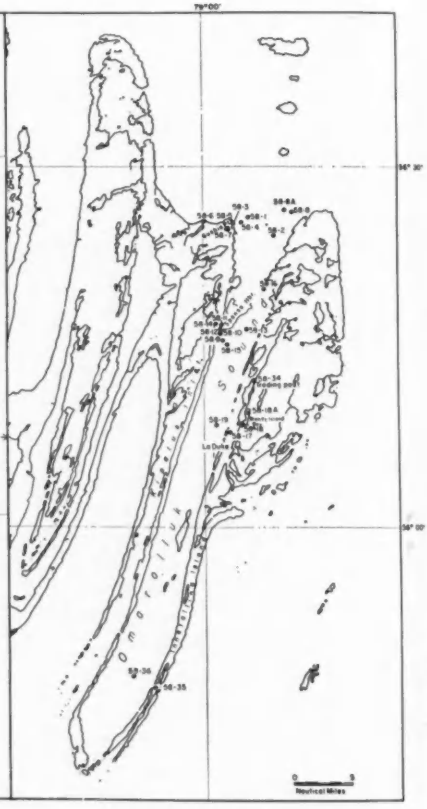

FIG. 7. Belcher Islands, Hudson Bay.

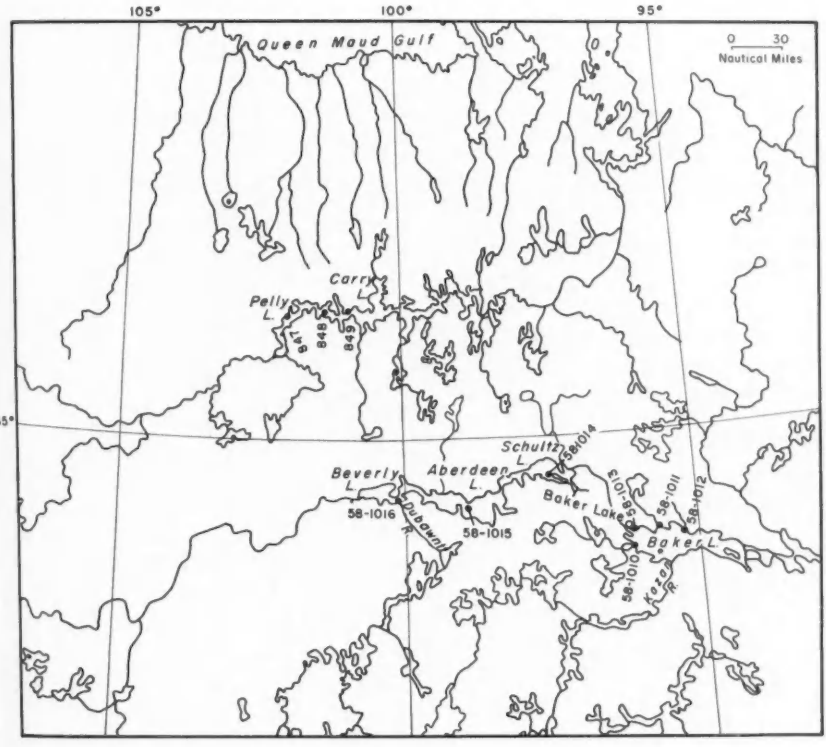

FIG. 8. Thelon and Back River systems.

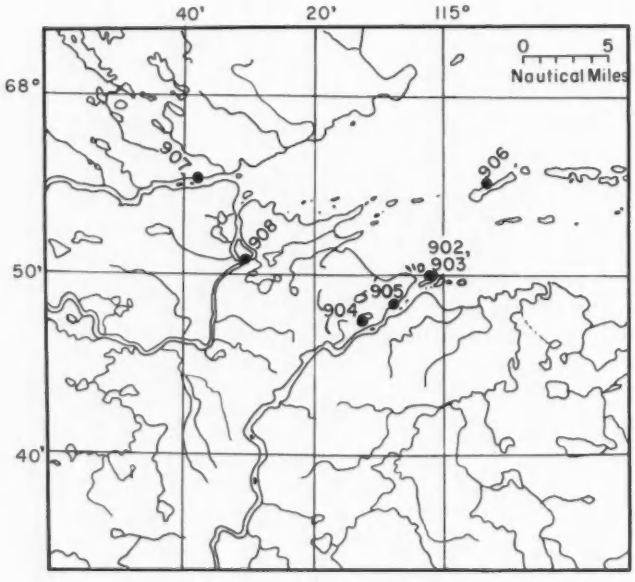

FIG. 9. Coppermine region.

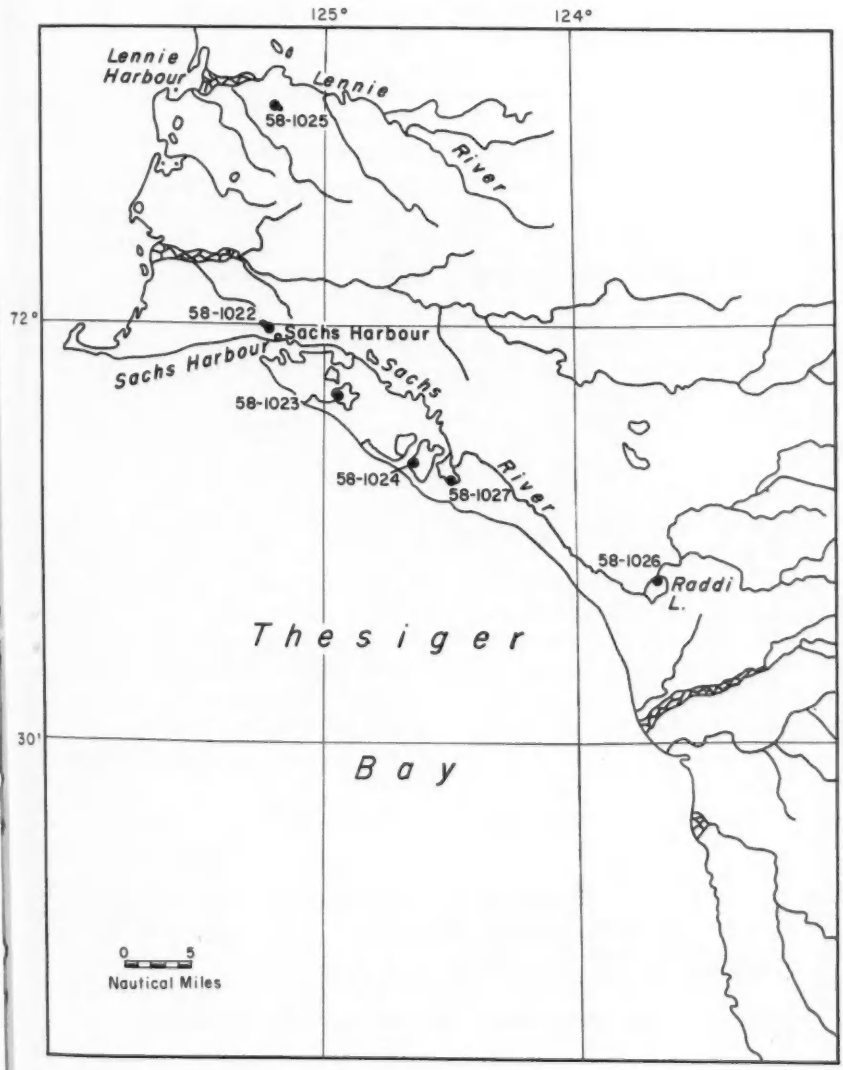

FIG. 10. Southwestern Banks Island.

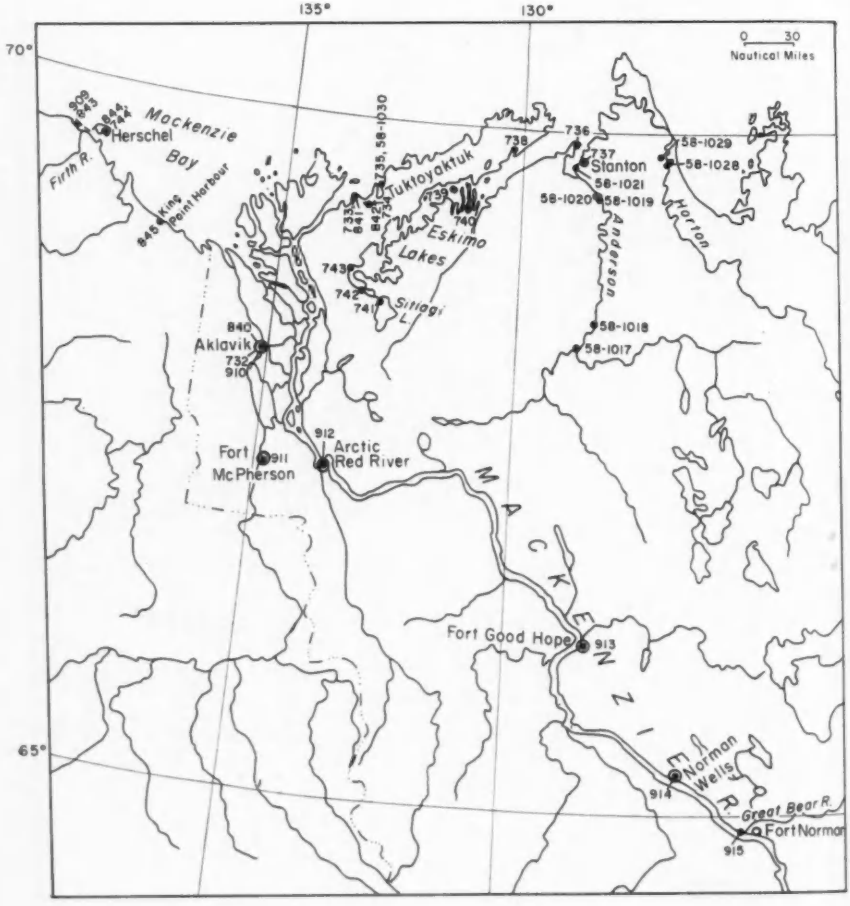

FIG. 11. Section of the Mackenzie River and coastal area adjacent to delta.

Biochemical Studies on Sockeye Salmon During Spawning Migration

VI. Ribonucleic Acid and Deoxyribonucleic Acid[1]

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ABSTRACT

The quantity of ribonucleic acid phosphorus (RNA-P) and deoxyribonucleic acid phosphorus (DNA-P) in various tissues of the sockeye salmon has been determined at three points in its spawning migration. During migration a net decrease in RNA-P and a net increase in DNA-P occurred in the whole fish of both sexes. Major losses in RNA-P occurred in the flesh, alimentary tract and milt, while major gains in DNA-P occurred in the milt and roe. In the combined head, skin, bones and tail large gains in both RNA-P and DNA-P took place.

INTRODUCTION

Apart from the work of Bluhm and Tarr (1957) on ribonucleic acid (RNA) and deoxyribonucleic acid (DNA) of the flesh, and of Emmanuel and Chaikoff (1953) on the DNA of milt, nothing has been published regarding the RNA and DNA content of other tissues of salmon (Tarr, 1958). As part of a program of investigation being carried out at this laboratory on the biochemistry of migrating salmon (Idler and Tsuyuki, 1958; Idler and Bitners, 1958; Duncan and Tarr, 1958; Wood, 1958; Idler and Bitners, 1959) the RNA and DNA content of the various tissues of sockeye salmon (*Oncorhynchus nerka*) at different stages of spawning migration has now been determined.

MATERIALS AND METHODS

Tissue Samples

The procedure by which samples were obtained has been described in detail (Idler and Tsuyuki, 1958). The samples examined in the present work were from the 1957 Fraser River run to Stuart Lake, and were portions of the same pooled samples that were used in previously described work (Idler and Tsuyuki, 1958).

Analyses

RNA and DNA in the tissues were separated by a modification of the procedure of Schmidt and Thannhauser (1945) as follows:

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A 5-g sample of tissue was homogenized at 1°C with 7.5 ml of distilled water. To the homogenate 25 ml of ice-cold *N* perchloric acid was added and the mixture was centrifuged 15 min in a refrigerated centrifuge at 10,300 × *g*. The supernatant solution was discarded and the residue washed twice with 35-ml portions of ice-cold *N* perchloric acid. The supernatant solutions were discarded and the residue was washed in turn (at 4°C) with 35 ml of 80% ethanol and 35 ml of 95% ethanol. The washings were discarded and the residue was boiled 3 min in 20 ml of ethanol–ethyl ether (3:1, v/v). The ethanol–ether was discarded and the process repeated. The residue was taken up in 15 ml of 0.3 *N* KOH (adjusted to pH 13.5 with 6 *N* KOH as necessary) and allowed to digest (with constant stirring) at 36°C for 18 hours. By this procedure the residues from all the salmon tissues examined were brought into solution. The digest was made 1 *N* in perchloric acid by the addition of ice-cold 70% perchloric acid and was allowed to stand 35 min at 1°C, after which the mixture was centrifuged 10 min at 10,300 × *g* in a refrigerated centrifuge. The supernatant solution was removed and retained and the precipitate was twice washed with ice-cold *N* perchloric acid. The washings were combined with the first supernatant solution. These combined solutions contained the digested RNA and will be referred to as the RNA fraction. To the precipitate, 5 ml of 0.5 *N* perchloric acid was added and the mixture heated 20 min at 70°C (Ogur and Rosen, 1950). The supernatant solution was separated and retained, and the process repeated with the residue. The two supernatant solutions were combined. These combined solutions will be referred to as the DNA fraction. With certain tissues different sized samples were used. When this occurred, the volumes of extractants were adjusted accordingly. For muscle, roe, and combined head, skin, bones and tail, etc., 15.0-g samples, and for spleen and heart, 4.0-g samples were used. With kidney, it was found desirable to carry out a third extraction with hot ethanol–ether to reduce the amount of fluorescing material present in the RNA fraction. The use of constant stirring during alkaline digestion in the Schmidt and Thannhauser procedure in the present work resulted from the observation that results for RNA were sometimes low and erratic when stirring was omitted.

RNA was measured by a procedure based on that of Davidson and Smellie (1952). The RNA fraction was adjusted to about pH 4 with 6 *N* KOH and the potassium perchlorate precipitated was removed by centrifugation. The precipitate was washed twice with ice-cold distilled water and the washings were combined with the initially separated solution. The precipitate was discarded. The combined solutions were concentrated to about 1.5 ml by the use of a flash-evaporator operated at 26°C. For this purpose a special flask fitted with a thick-walled capillary tubing tip, calibrated in 0.1-ml graduations, was used. By means of low-speed centrifugation and washing of the sides of the flask with small volumes of water, the whole of the concentrated RNA fraction was collected in the tip of the flask and thus its total volume and the volume occupied by the small amount of potassium perchlorate precipitate present at this stage could be measured. Both values were recorded, and in subsequent calculations corrections were made for the space occupied by the precipitate, after first converting the measured volume it

occupied to its actual volume by means of an empirically determined factor. Suitable aliquots of the concentrated RNA fraction, in duplicate, were subjected to electrophoresis on Whatman #3 paper in 0.25 *M* ammonium formate buffer pH 3.5 at 25 volts/cm and 8°C for 2 to 2½ hours. Spots containing nucleotides were located by means of an ultraviolet lamp, cut out and eluted for 1½ hours at 30°C in 3 ml of 0.5 *M* sodium phosphate buffer, pH 7.0. The optical density of each solution was determined with a Beckman DU spectrophotometer at appropriate wavelengths in the ultraviolet region. Reference blanks were prepared from pieces of nucleotide-free paper adjacent to, and of the same size as the spot-containing areas. The quantity of each nucleotide was calculated by means of the absorption data of Elson *et al.* (1954). By combining the values found for the four mononucleotides the total amount of RNA phosphorus in the tissue was determined.

For determination of DNA phosphorus, suitable aliquots of the DNA fraction (made up to 3 ml when necessary with 0.5 *N* perchloric acid) were digested with 1 ml of 70% perchloric acid. The volume of the digest was brought to 10 ml with distilled water and phosphorus determinations were made on suitable aliquots by the method of King (1932).

Before the above procedures were adopted for use in the present work, certain alternative methods of both extraction and measurement were investigated. One of these (Schneider, 1945) entailed a hot acid extraction of RNA and DNA together from the tissue, followed by determination of the two nucleic acids by specific colour reactions for ribose and deoxyribose. When applied to salmon flesh the procedure yielded very low values for ribose—about 12% of that found with the Schmidt and Thannhauser procedure. The value, although it remained low, could be increased by lengthening the extraction time to 60 min from 15 min, but when the time was increased beyond this, the value decreased. It appeared that ribose was being destroyed during the extraction procedure, presumably by reaction with the protein present. Another procedure (Ogur and Rosen, 1950) involved separation of RNA from DNA by cold acid extraction of RNA from the tissue followed by extraction of DNA from the residue with hot acid. This procedure gave poor separation of the nucleic acids when applied to salmon muscle, apparently because of incomplete extraction of RNA in the first step. The Schmidt and Thannhauser procedure provided good separation of RNA from DNA when applied to salmon muscle. No DNA was detected in the RNA fraction by means of the diphenylamine reaction for deoxyribose (Racker, 1952). For measurement of DNA in the DNA fraction, the indole reaction (Keck, 1956) and the diphenylamine reaction (Racker, 1952) for deoxyribose, and phosphorus analysis were investigated. Each of these three methods requires for calculation of the amount of DNA the use of a factor that is dependent on the composition of the DNA. This will probably vary from tissue to tissue. Thus, for each tissue a separate DNA standard would be required and such standards are not available. To illustrate the difficulty involved, the only DNA standard available was from salmon sperm. When this was used in connection with the analysis of salmon flesh, the phosphorus analysis indicated the presence of only 84% as much DNA as was found by the other methods. Of the three methods, only phosphorus analysis is known to determine

the total amount of the particular component of DNA being measured, and thus, of the three, it is the only one yielding results that are meaningful in themselves without the use of further calculation. For this reason phosphorus analysis was used in the present work. For measurement of RNA following its digestion in the Schmidt and Thannhauser procedure, the orcinol colour reaction (Mejbaum, 1939) and the cysteine–sulphuric acid reaction (Dische, 1949) were investigated. Each was found to be interfered with by unidentified material present in the digest, and for this reason the much more specific procedure involving determination of the mononucleotides (Davidson and Smellie, 1952) was used, although this is known to yield values about 6% low (Smith, 1955).

RESULTS AND DISCUSSION

As preliminary work indicated that the results of determinations made on different groups of fish obtained at one station were in agreement with each other within ± 6%, analyses were made on the tissues from only one of the groups of fish of each sex taken from each of the three points along the route of migra-

TABLE I. Ribonucleic acid phosphorus in the tissues of migrating sockeye salmon.

Tissue	Sex	Point in migration					
		Lummi Is.		Lillooet		Forfar Creek	
		RNA-P per 100 g tissue	Total[a] RNA-P in tissue	RNA-P per 100 g tissue	Total RNA-P in tissue	RNA-P per 100 g tissue	Total RNA-P in tissue
		mg	*mg*	*mg*	*mg*	*mg*	*mg*
Alimentary tract	M	32.8	29.8	24.1	7.1	17.5	2.8
	F	36.9	28.8	26.3	6.8	20.5	2.5
Flesh	M	6.4	93.3	4.7	61.1	4.7	60.5
	F	7.0	93.9	5.2	59.2	5.1	47.1
Gonads	M	43.5	24.5	34.5	28.2	17.4	14.9
	F	3.9	3.1	3.6	5.0	2.0	5.9
Head, skin, bones, tail, etc.	M	6.6	58.3	6.4	55.2	8.6	90.8
	F	6.1	47.7	5.4	41.5	7.0	58.6
Heart	M	10.1	0.6	10.6	0.6	11.3	0.6
	F	11.4	0.6	10.6	0.6	11.2	0.6
Kidney	M	29.7	7.8	33.8	7.8	31.4	8.7
	F	27.5	6.2	33.8	6.8	33.4	6.5
Liver	M	81.7	25.7	75.7	19.2	75.4	28.2
	F	106.7	42.8	116.1	51.8	121.3	49.0
Spleen	M	37.2	0.9	33.5	0.6	25.9	0.9
	F	35.4	0.6	37.7	0.6	35.6	0.8
Total for whole fish	M	—	240.9	—	179.8	—	207.4
	F	—	223.7	—	172.3	—	171.0

[a]The tissue weights used in the calculations were taken from tables II and III of the paper by Idler and Tsuyuki (1958).

tion. For the heart and spleen, due to the limited quantity of these tissues available, the analyses were made on a sample (for each sex) obtained by combining 1-g amounts from each of the four groups.

The results of the RNA determinations are recorded in Table I, and may be summed up as follows:

Alimentary tract and flesh. There was a marked loss in total RNA in both sexes in each of these tissues during migration. The greater part of the loss occurred between Lummi Island and Lillooet. The concentration of RNA in these tissues also decreased.

Heart, kidney, liver and spleen. The total RNA in each of these tissues did not appear to change greatly during migration. An interesting point here was the much greater concentration and total amount of RNA found in the liver of the female than in that of the male.

Gonads. The quantity of RNA in the roe nearly doubled during migration, while in the milt there was a decrease in total RNA.

Head, skin, bones, tail, etc. There was an increase in RNA in these combined tissues during migration.

The results of DNA determinations (Table II) may be summarized as follows:

Alimentary tract. For both sexes there was a loss in total DNA in this tissue. DNA was lost more slowly than the tissue as a whole and this led to an apparent increase in DNA concentration.

Gonads. There was an increase in total DNA in both milt and roe.

Head, skin, bones, tail, etc. In these combined tissues there was an increase in total DNA.

Flesh, heart, kidney, liver and spleen. The changes in quantity of DNA in these tissues were relatively small and somewhat irregular.

In the whole fish of either sex there was a net loss in RNA and a net gain in DNA during migration. In males the gain in DNA exceeded the loss in RNA, while in females the gain in DNA was very much less than the loss in RNA.

It is interesting to compare the data for salmon with the available data for mammalian tissues (Leslie, 1955). The RNA concentrations found in salmon heart, kidney, spleen and male liver fell within the ranges reported for these tissues in various mammals, while the RNA concentration in female liver was a little higher. The RNA and DNA concentrations in salmon flesh were somewhat less than those in mammalian flesh. For heart, liver and spleen the DNA concentrations in salmon fell within the ranges for these tissues in mammals, but for kidney the concentration in salmon was higher than that reported for mammals. The ratios of RNA to DNA found in these salmon tissues were similar to those in mammalian tissues. The ratios in flesh, liver and spleen for salmon fell within

TABLE II. Deoxyribonucleic acid phosphorus in the tissues of migrating sockeye salmon.

Tissue	Sex	Point in migration					
		Lummi Is.		Lillooet		Forfar Creek	
		DNA-P per 100 g tissue	Total[a] DNA-P in tissue	DNA-P per 100 g tissue	Total DNA-P in tissue	DNA-P per 100 g tissue	Total DNA-P in tissue
		mg	*mg*	*mg*	*mg*	*mg*	*mg*
Alimentary tract	M	18.5	16.7	26.5	8.1	32.3	5.3
	F	19.9	15.5	29.3	7.8	28.6	3.7
Flesh	M	2.7	39.7	2.5	32.0	2.4	31.0
	F	2.1	28.2	2.1	23.9	3.3	30.7
Gonads	M	236.0	133.3	268.0	220.0	226.0	192.0
	F	2.9	2.2	2.6	3.7	2.1	6.2
Head, skin, bones, tail, etc.	M	2.9	25.4	4.2	36.6	4.4	46.8
	F	2.7	21.1	4.5	34.4	5.4	45.0
Heart	M	20.0	1.2	20.2	1.2	15.5	0.9
	F	20.4	0.9	17.1	0.9	16.5	0.6
Kidney	M	59.2	15.5	67.2	15.5	59.2	16.7
	F	70.6	15.2	61.6	12.1	67.2	13.3
Liver	M	40.8	13.0	46.8	11.8	30.8	11.5
	F	37.2	14.9	30.0	13.3	42.8	17.4
Spleen	M	94.1	2.8	101.0	1.9	88.1	3.1
	F	83.5	1.6	91.6	1.2	95.2	2.2
Total for whole fish	M	—	247.6	—	327.1	—	307.3
	F	—	99.6	—	97.3	—	119.1

[a]The tissue weights used in the calculations were taken from tables II and III of the paper by Idler and Tsuyuki (1958).

the ratios recorded for mammals, while the ratio in salmon heart was a little lower and that in salmon kidney considerably lower than the lowest values reported for mammals. The low ratio in salmon kidney resulted from the unusually high DNA concentration in this organ.

The ratios of the nucleotides found in the alkaline hydrolysates of the various tissues are shown in Table III. With certain exceptions the ratios for different tissues were similar to each other. The RNA of spleen and kidney had a higher content of uridylic acid than did the RNA of other tissues. Similarly the RNA of roe, and of the combined head, skin, bones and tail, etc., had a higher content of guanylic acid. The RNA of milt of fish taken at Lummi Island and Lillooet was lower in guanylic acid than was that of the fish taken at Forfar Creek. This difference may be related to the fact that there was a large decrease in total RNA in the milt between Lillooet and Forfar Creek. The RNA of the spleen, particularly of female fish, had less guanylic acid at Lillooet than at the other two points in migration. No satisfactory explanation of this irregularity can be advanced at present, but it should be noted that the spleens of both sexes were lighter in weight at Lillooet than at the other two points (Idler and Tsuyuki, 1958). The ratio of the nucleotides found for the RNA of flesh in the present work differs

TABLE III. Ratios of ribonucleotides in the RNA of migrating sockeye salmon.

Tissue	Sex	Point in migration											
		Lummi Is.				Lillooet				Forfar Creek			
		C[1]	A	G	U	C	A	G	U	C	A	G	U
Alimentary tract	M	1.14	1.00	1.24	1.03	1.26	1.00	1.48	0.99	1.20	1.00	1.40	0.96
	F	1.05	1.00	1.11	0.84	1.19	1.00	1.35	0.98	1.20	1.00	1.38	0.93
Flesh	M	1.19	1.00	1.46	0.81	1.22	1.00	1.48	0.88	1.27	1.00	1.38	0.68
	F	1.26	1.00	1.44	0.91	1.15	1.00	1.39	0.76	1.32	1.00	1.46	0.89
Gonads	M	1.17	1.00	0.93	0.93	1.16	1.00	0.93	0.86	1.24	1.00	1.39	0.98
	F	1.34	1.00	1.45	0.79	1.14	1.00	1.69	0.78	1.24	1.00	1.59	0.85
Head, skin, bones, tail, etc.	M	1.25	1.00	1.56	0.83	1.22	1.00	1.67	0.68	1.31	1.00	1.66	0.92
	F	1.34	1.00	1.76	0.70	1.20	1.00	1.58	0.77	1.16	1.00	1.53	0.95
Heart	M	1.20	1.00	1.38	0.95	1.20	1.00	1.25	0.92	1.18	1.00	1.47	0.93
	F	1.39	1.00	1.38	0.99	1.18	1.00	1.21	0.82	1.19	1.00	1.41	0.91
Kidney	M	1.23	1.00	1.33	1.05	1.21	1.00	1.44	0.85	1.11	1.00	1.60	1.14
	F	1.21	1.00	1.00	1.03	1.24	1.00	1.26	1.03	1.21	1.00	1.46	1.22
Liver	M	1.21	1.00	1.41	0.91	1.16	1.00	1.49	0.98	1.09	1.00	1.50	0.95
	F	1.18	1.00	1.42	0.93	1.25	1.00	1.39	0.96	1.22	1.00	1.47	1.01
Spleen	M	1.28	1.00	1.36	1.08	1.26	1.00	1.20	1.18	1.23	1.00	1.47	1.04
	F	1.24	1.00	1.48	1.06	1.11	1.00	0.94	0.95	1.17	1.00	1.47	1.01

[1]Abbreviations: C = cytidylic acid; A = adenylic acid; G = guanylic acid; U = uridylic acid.

considerably from that previously reported for RNA isolated from sockeye salmon flesh (Bluhm and Tarr, 1957). The reason for this may lie in a possible preferential extraction of a particular RNA fraction in the latter work, as it is known that different base ratios occur in separable fractions of RNA from animal tissues (Magasanik, 1955).

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Fatigue and Mortality in Troll-Caught Pacific Salmon (*Oncorhynchus*)[1,2,3]

By R. R. Parker[4], E. C. Black[5] and P. A. Larkin[6]

ABSTRACT

Capture by trolling subjects feeding coho and chinook salmon to hyperactivity which may lead to a distressed condition or death, and death cannot be predicted from examination of individual fish at time of capture. Mortality of coho was estimated to be in the 0.95 confidence interval of 34% and 52%. Time of maximum death rate of coho is shown to coincide with the period of maximum blood lactate response. Survival occurred either when blood lactate did not reach critical levels (above 125 mg%) or reached critical levels and subsequently subsided. Holding salmon in a live box for 8–14 hours before release did not improve tag recovery, suggesting additional indiscriminant stress was caused at release. Adult coho in fresh water did not appear capable of lethal hyperactivity. This led to the hypothesis that cessation of feeding during spawning migration has adaptive significance for survivial of Pacific salmon.

INTRODUCTION

That fish die in captivity following strenuous muscular exertion has been demonstrated by several authors. Among these are von Buddenbrock (1938) working with cod (*Gadus morrhua*) and dab (*Platessa limanda*); Secondat and Diaz (1942) with tench (*Tinca tinca*); Milne and Ball (1956) with coho salmon (*Oncorhynchus kisutch*) and later (1958) with both coho and chinook (*O. tshawytscha*); Black (1957c) with sockeye (*O. nerka*); Bates and Vinsonhaler (1957) with smolt chinook, striped bass (*Roccus saxatalis*), and shad (*Alosa sapidissima*); Fry (1958) with coho and chinook; and Parker and Black (1959) with chinook. In every case severe muscular activity was followed by significant mortality.

Other authors have subjected these and other species to severe fatigue and have not observed significant ensuing mortality. Included here are Black (1957a,b) working with rainbow trout (*Salmo gairdnerii*) and lake trout (*Salvelinus namaycush*). Paulik, DeLacy and Stacy (1957) working with coho, and Paulik and DeLacy (1958) with sockeye repeatedly subjected their animals to exhaustion without resulting significant mortality. Jensen (1958) hooked and released salt-water-pond-reared chinook without significant mortality. Black (1958b) has reviewed the subject of hyperactivity and death. The specific causes of mortality have not been determined. Why fatigue should in one case lead to mortality, and in another case, not, remains a mystery.

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It has been suggested by colleagues that mortality in live boxes of fatigued fish reported by Parker and Black (1959) was caused by factors other than fatigue, *viz.* unrecognized injury, psychosis from enclosure in small space or from handling, breaking the mucous coat, etc. Perhaps a summation (Brett, 1958) of these stresses[7] is responsible. The validity of extrapolating mortality observations in holding experiments to apply to fish caught and released after tagging, or released because of size limit restriction is thus open to question. However, investigators have repeatedly shown tag recoveries of less than 30% for troll-caught salmon (Milne, 1957) released in the face of a fishery known to be much more intensive.

For example, Parker and Kirkness (1956) tagged selected chinook salmon, apparently unharmed and predominantly of Columbia River origin. For fish in their ultimate year recoveries were only 21%, yet from data of Silliman (1948, 1950) it can be estimated that a total fishing mortality of Columbia River chinook averaged 86% per annum over the 11 years 1935 to 1945. A total non-fishing mortality (or tag loss which was known to be minimal) of over 70% is necessary to account for this difference. Parker and Kirkness (1956) estimated average annual natural mortality to be approximately 34%. Thus, a mortality in excess of 45% remains unaccounted for by this rough approximation.

Secondat and Diaz (1942) reported that blood lactate concentrations of tench increased following forced activity but usually subsided by the end of 6 hours. They also observed that some fish died and blood lactate levels of these had failed to decrease. Black (1955, 1957a,b,c) demonstrated a similar response for several species of salmonids; in general, blood lactate levels continued to increase during post-exercise rest periods, and peak values were attained during the second or third hour of post-exercise rest. Blood lactate levels then decreased at a decelerating rate. Resting levels were not attained before 12 hours. This sequence is termed "typical response". Black (1957c) suspected a correlation between death and concentration of blood lactate, but lacked sufficient data for a conclusive demonstration. Parker and Black (1959), working with troll-caught chinook, demonstrated a positive association between blood lactate levels and death. While high blood lactate levels have not been shown to be a primary cause of death, they are a significant correlate of death following hyperactivity.

It is the purpose of this experiment to extend these observations to include coho salmon, to further explore the significance of death as related to hyperactivity and to examine the problem in both salt and freshwater environments.

METHODS AND MATERIALS

Ocean Study

Fish were obtained aboard a commercial troller operating in the Gulf of Alaska in 1958. During July fishing was in the vicinity of the coast at Cross Sound (Lat 58°N) and in August in the vicinity of Middleton Island (Lat 60°N,

[7]The word *stress* is used in this paper meaning any trauma and does not imply change in anterior pituitary–interrenal activity, although this may be involved.

Long 147°W). Either 4 or 6 lines were used (depending upon the distance off shore) and from 8 to 12 lures per line. Lures were changed often and no general statement can be made of make and type. Hook size ranged from No 6 to No 8. Time, place and manner of fishing were at the discretion of the Captain.

Captured fish were lifted aboard by the lure and placed in a preliminary bath of sea water where the hook was carefully removed. Fish showing damage to vital parts or heavy bleeding were excluded from further consideration except to obtain blood samples from specimens without post-exercise rest. All non-critically damaged fish were tagged at the origin of the dorsal fin, using standard Peterson type tags with $\frac{5}{8}$-inch red baffles and pure nickel pins.

Fish to be retained in captivity were transferred to a live box measuring 28¼ by 44¼ inches (72 × 112 cm) inside horizontally and 23¼ inches (60 cm) between top and bottom. Access to the inside was through a 12 by 12-inch (30 cm square) chimney, 8 inches (20 cm) high and fitted with a removable cover. Water was introduced under pressure at the bottom and expelled through holes drilled in the top panel. The water level was approximately 4 inches (10 cm) in the chimney, which prevented sloshing or surge in the main box. Two identical boxes were used, and each was supplied with fresh sea water at a rate of approximately 10 U.S. gallons (39 l) per minute. The top was fitted with a 12 by 12-inch (305 × 305 mm) plexiglass panel through which fish could be observed. A maximum of 4 fish or less than 40 lb (18 kg) of fish was held in a live box at any one time.

Fish which died in the live box were removed with a small gaff and a blood sample taken. Cessation of respiratory movement was used as a criterion of death. Fish were under more or less constant observation and blood samples were obtained before *rigor mortis*. Survivors were liberated without taking a blood sample. To do this, the water supply to the live box was cut off and contents drawn down to approximately 50 U.S. gallons (190 1). A sedative (Tricane methane sulfonate, MS222 Sandoz) was introduced into the water, and as soon as fish became disorientated they were removed by means of a polyethylene bucket and liberated. This method of release was unsatisfactory because (a) fish were unable to orient themselves for some minutes until the effects of the sedative wore off and (b) fish in live boxes one-third full were subject to severe sloshing, depending upon the state of the sea (seldom smooth). With the equipment at hand, however, the alternative of subjecting them to chase and struggling in a dip net appeared to be even less satisfactory.

One millilitre or less of blood was drawn routinely from the caudal vein. In some instances samples were also drawn from the heart. Blood was drawn into a 2-ml Luer syringe coated with mineral oil and rinsed with heparin solution. The sample was immediately expelled into a polyethylene bottle containing 9 ml of 10% trichloracetic acid. This mixture was then filtered and the filtrate stored in a second polyethylene bottle until chemical analysis. These samples were taken to the laboratory at the University of British Columbia and analysed for lactic acid by the method of Barker and Summerson (Hawk, Oser and Summerson, 1949). Values of blood lactate are reported as milligrams lactic acid per

100 ml of whole blood (mg%) and expressed to three integers. The true value, as determined from analysis of several triplicated determinations, is considered to be within a range of ± 10 mg%.

Live box sea water was drawn from a depth of approximately 1.5 m and was between 13° and 15°C. Fishing ranged over depths from 20 to 100 m. Salmon were taken at all depths, but coho more frequently above a depth of 30 m and in water ranging from 10° upward, while chinook were more frequently below 30 m and at 7–10°C. Reliable temperature data could not be taken for individual fish and the significance of temperature changes cannot be evaluated.

Fish used were feeding coho and chinook. Coho were in their ultimate year but not showing sexual dimorphism typical of the species at maturity. Gonad examination showed signs of approaching maturity and tagging showed fairly rapid subsequent movement into inside waters. Chinook used were probably either in their ultimate or penultimate year of life.

Fish were disturbed as little as possible during the rest period. Design of the live boxes eliminated sloshing due to vessel motion, but vibration from the propulsion engine was present. When first placed in the live box, fish would generally swim about but quickly assumed and maintained a position. Some fish failed to maintain equilibrium and remained upside down either at the surface or bottom. This condition usually appeared after 15–30 minutes although a few individuals turned over when first placed in the live box. Some fish righted themselves after varying amounts of rest, others failed entirely to do so. These observations are similar to those made by Brett *et al.* (1958) on fatigued juvenile sockeye and coho in freshwater, and by Parker and Black (1959) on sub-adult chinook in sea water.

An attempt was made to determine the amount of time each fish spent on the troll gear but was largely unsuccessful, either because of failure to observe the strike or inability to discriminate between several fish caught on the same line. From the reliable data available, coho were on the gear for an approximate average of 5 minutes, and the time varied from less than 2 to more than 25 minutes. Coho were of a fairly uniform size, averaging 8 lb (3.6 kg) and varying from 6 to 10 lb (2.7 to 4.5 kg). Chinook used varied between 8 and 20 lb (3.6 to 9.1 kg).

Freshwater Study

In September the live boxes and equipment were taken to the Canyon Island Research Station 17 miles above salt water on Taku River, Alaska. Upstream migrating adult coho were captured by a fish-wheel (Anon., 1953) and used as test animals. These fish were of the same size range as those used in the ocean study, were non-feeding, in an advanced stage of sexual dimorphism, and were in freshwater. The live boxes were set up on the pontoons of the fish-wheel and river water pumped at approximately the same rate as in the previous experiment at sea. A pole was fixed to overhang the stream and standard troll gear with a 20-lb (9.1 kg) weight attached. This device was used to simulate the action of troll gear towed through the water. Stream velocity was approximately

equivalent to trolling speed. Fish were dip-netted from holding tanks, a hook was inserted from inside the mouth through the membranes and tissue posterior to the maxillary, and the fish was then released into the river attached to the troll gear. After intervals from less than one and up to 30 minutes on the troll gear fish were landed by the lure and placed in a preliminary water bath containing sedative. Here the hook was removed, the fish tagged, and then placed in a live box. A maximum of 6 fish or 60 lb (27 kg) was placed in each box. Groups were anaesthetized and removed from the live boxes after post-exercise rest periods over a range of zero to 52 hours, and a blood sample was taken by caudal vein puncture. Sampled fish were further observed until recovery from the anaesthetic and then released into the river. A control group was dip-netted from the tanks directly into the sedative bath and sampled. Other aspects of the experiments were identical with the ocean study.

SUB-MATURE COHO IN SEA WATER

Blood was drawn from both the caudal vein and the heart of 11 coho to facilitate comparison between the present experiment and those of Black (1957c) and Parker and Black (1959). Three determinations were made on each sample and values of heart and caudal vein blood lactate compared. Table I gives the

TABLE I. Repeated determinations of blood lactate levels from the caudal vein and heart of each of 11 coho caught by troll in salt water. Values in parentheses are estimated dummy values for ease in computation.

Sampled immediately after hooking			Sampled 1 to 5 hours after hooking		
Specimen	Heart	Caudal	Specimen	Heart	Caudal
	mg%	*mg%*		*mg%*	*mg%*
	15.7	12.3		155.	171.
1	15.7	13.7	8	162.	165.
	(15.7)	(13.0)		150.	168.
	62.4	60.8		180.	172.
2	63.0	62.5	9	170.	172.
	(62.7)	(61.6)		166.	172.
	120.	86.0		112.	118.
3	121.	94.5	10	107.	113.
	121.	99.0		109.	113.
	75.6	49.6		234.	238.
4	90.5	60.9	11	250.	248.
	80.0	65.5		248.	245.
	43.0	31.7			
5	48.7	30.6			
	42.5	30.2			
	38.8	31.2			
6	43.0	32.3			
	39.8	(31.7)			
	63.0	57.4			
7	64.4	59.9			
	63.7	59.5			
Mean	61.44	49.71		170.3	174.6

results of the determinations. Caudal vein blood lactate levels were significantly lower than heart blood lactate levels in the 7 fish sampled immediately after catching ($F = 9.01$; df 1, 6; $0.01 > P > 0.025$). In the 4 fish sampled after 1 to 5 hours of rest caudal levels were slightly higher than heart levels but differences were not significant ($F = 2.13$; df 1, 3; $0.10 > P > 0.25$). Thus the degree of blood lactate response may appear greater in the coho than reported for sockeye and chinook, but the anomaly may be due to the anatomical sampling location.

Blood Lactate Levels

Eleven coho were killed immediately when landed to establish a post-exercise base level. One fish died in the live box in less than ½ hour and is included in the first group. Fish were held in live boxes up to 14 hours. During this time 48 additional fish died, 47 of which were sampled for blood. These are grouped into half hour time periods including the time on the gear. Where this statistic is unknown (8 cases), average time spent on the gear is used (4.74 min, $n = 50$). Table II gives average values and ranges for time and blood lactate

Table II. Blood lactate levels of troll-caught coho salmon which died during post-exercise period.

Number	Time period from hooking			Lactic acid		
(*n*)	Average	Range		Average	Range	
	hours			*mg%*		
12*	0.10	0.03	0.43	53.3	13.0	93.2
4	0.78	0.57	0.92	156.	123.	236.
12	1.20	1.03	1.42	187.	133.	273.
9	1.65	1.50	1.83	211.	147.	282.
9	2.25	2.03	2.50	209.	158.	280.
4	2.75	2.58	2.92	195.	154.	240.
1	3.25	...	...	298.	...	...
2	4.28	4.27	4.32	292.	280.	304.
1	4.92	...	...	224.	...	...
2	5.27	5.17	5.42	220.	180.	260.
2	5.53	...	...	265.	212.	318.
1	8.88	...	...	219.	...	...

*Eleven fish included in the first time period were killed and sampled when landed. The remainder are fish which died in the live boxes.

values. These data are presented graphically in Fig 1. A typical delayed blood lactate response is depicted. Blood levels of lactate increased at least 4-fold from pre-exercised levels. In this study lactate levels did not subside; however, these samples are from fish which died. Lactate in the blood of a single normal-appearing specimen deliberately killed in the fifth hour was 115 mg%. While not by itself sufficient evidence, this relatively low value of blood lactate in a survivor is substantiated by previous work with chinook (Parker and Black, 1959).

MORTALITY

During the course of the experiment 49 fish died. As 26 fish were released during the time periods when deaths occurred, the simple ratio, 49/115, is not a valid estimate of mortality. Further, the problem of setting confidence limits is complicated by a decreasing sample size. Because the solution to this statistical

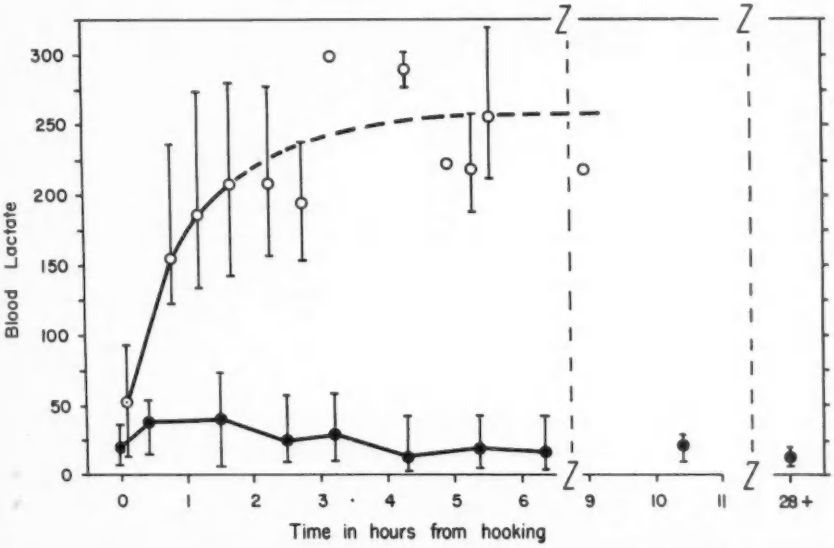

FIG. 1. Coho blood lactate (expressed as mg% lactic acid) response in time from hooking. Open circles represent mean value for fish which died in the salt water experiment. Dashed line drawn freehand to indicate probable average. Solid circles represent mean value for fish in fresh water. Vertical lines through means indicate range of values.

problem has a general applicability to a variety of similar problems it is presented in detail as an Appendix. The results, together with the original observations, are summarily presented in Table III. Two points are of special interest. First, the highest rate of mortality took place in the second and third hours after hooking. Second, mortality was substantially complete (97%) by the end of 6 hours.

RECAPTURE OF TAGGED FISH

If observed mortalities on troll caught salmon held in live tanks aboard the vessel are representative of mortality experienced by lots of fish released immediately after capture, then survivors of lots held past the mortality period should show a higher percentage recaptured than those released immediately. This hypothesis was explored by releasing 60 fish immediately after capture and 40

fish held 9 hours or longer (Table III). Recoveries were entirely from subsequent commercial fishing and while probably not completely reported at time of analysis (October, 1958) no substantial change can be expected. Twelve of the first group and 7 of the second have been recaptured.

TABLE III. Mortality of coho salmon during post-exercise rest period.

Time period	Fish at start of period (n)	Deaths during period (y)	Released during period	Instantaneous mortality rate (i)	Cumulative total mortality		
					Point estimate	Confidence interval	
					Q	$\underline{Q}$	$\bar{Q}$
hours	*no.*	*no.*	*no.*				
0–1	115	5	0	0.044	0.044	0.006	0.080
1–2	110	21	0	0.212	0.226	0.146	0.299
2–3	89	14	2	0.171	0.348	0.255	0.429
3–4	73	1	0	0.038	0.357	0.263	0.438
4–5	72	3	6	0.043	0.384	0.288	0.474
5–6	63	4	7	0.066	0.423	0.330	0.507
6–7	52	0	5	0	0.423	0.330	0.507
7–8	47	0	6	0	0.423	0.330	0.507
8–9	41	1	0	0.025	0.437	0.336	0.522
9–14	40	0	40	0	0.437	0.336	0.522
Total		49	66				

Although these data are apparently homogeneous, many of the fish which recovered in the live boxes were disoriented for varying lengths of time and one might expect that fish which were released immediately would not only suffer the same mortality as those which were held but an additional mortality associated with disorientation i.e. loss to predators. As stated in a previous section, there was reason to consider the releasing procedure unsatisfactory. Further studies are needed on proper techniques for testing the hypothesis.

ADULT COHO IN FRESH WATER

This phase of the experiment was designed to test the significance of time spent on the gear in relation to levels attained by blood lactate and its associated mortality, and to compare these results for fish in freshwater which have undergone physiological changes of approaching maturity (Hoar, 1957) with those of fish feeding in the ocean. In this experiment it was possible to have relatively unexercised fish which were not obtainable in the ocean study. Results are summarized in Table IV.

Blood lactate increased from the control level two-fold in the first 2 hours, then subsequently fell to a level below that of the controls in the fifth hour. This typical response is depicted in Fig 1 where it may be compared with the lactate response of coho in the ocean study. It is obvious that lactate concentrations at no time approached those of fish dying in the live boxes at sea. Equally apparent is the decrease in range of lactate values as fish were held for longer periods.

TABLE IV. Blood lactate levels of coho salmon during post-exercise period in fresh water. (Exercise time, varying from less than 1 minute to 30 minutes, is included in the "post-exercise" period.)

Number of specimens	Time period			Lactic acid		
	Average	Range		Average	Range	
	hours			*mg%*		
25	Control (unexercised)			20.20	8.2	37.5
27	0.427	.05	.95	38.07	15.2	54.3
30	1.488	1.11	2.00	40.07	7.7	74.5
23	2.455	2.05	2.82	24.62	9.1	58.8
18	3.213	3.02	3.72	28.78	7.7	64.6
15	4.285	4.01	4.93	13.89	3.3	42.8
12	5.357	5.08	5.83	19.50	3.4	43.9
15	6.343	6.01	6.96	17.05	4.0	43.6
13	10.434	9.98	10.99	21.86	9.3	29.7
12	28 hours and more			12.46	7.2	19.6

Multiple regression analysis was used to test the effect of time spent on the hook on the lactate response. Controls and fish held longer than 5 hours were excluded from the data; mean levels of blood lactate approximate a linear regression on time for the segment 0.05 to 5.0 hours of total time. The regression, in ordinary units, is:

$$\hat{Y} = 43.855 - 6.297X_1 + 2.396X_2$$

where $\hat{Y}$ estimates the blood lactate level,

X_1 is the total time from start of exercise to sampling,

X_2 is the total time spent on hook.

The standard regression of Y on X_1 independent of X_2 proved significant (t of $b'_{y1.2} = 5.676$; d.f. 1,10; $P < 0.01$); however the lactate response was not significantly influenced by the amount of time spent on the hook (t of $b'_{y2.1} = 0.269$; $P > 0.5$). This observation is interpreted to mean that the initial struggle from hooking plus final struggle of unhooking elicited maximum response of blood lactate that fish were capable of producing.

Blood lactate levels from 0.05 to 0.5 hours were tested against the control group by analysis of variance and found significantly higher ($F = 14.87$; d.f. 1, 39; $P < 0.01$). Similar treatment shows blood lactate was significantly lower in fish held 28 hours or more than in the control group ($F = 7.38$; d.f. 1, 36; $P < 0.01$). Thus the control group reflected blood lactate present from either work done in swimming against the river current or in initial excitement in the fish-wheel holding tanks.

While exposed to treatment similar to the salt water group, fish in these experiments did not respond with the same degree of violence on the gear. They appeared to be content to swim the same speed as the current and made few rushes against the gear. When landed they struggled less violently than their salt water counterparts. This was reflected in the blood lactate levels which in no case increased above 77.5 mg%. Further, *not one fish died* during the experiment. The type of blood lactate response was the same for both groups but the degree of response was much less for the freshwater group.

OCEAN CHINOOK

Secondat and Diaz (1942) followed the rise and fall of blood lactate of tench by taking 3 consecutive samples of blood from each fish; the first immediately after exercise, the second at 2 hours, and the third at 6 hours. Cardiac puncture was used. Subsequent workers have taken blood samples only from stunned, killed, or dying fish (Black, 1955, 1957a,b,c; Nakatani, 1957; Parker and Black, 1959), and from these data it has been *deduced* that blood lactate level of survivors has at first risen and then declined . While there is little doubt of the type of response, actual evidence that blood lactate has been at concentrations equal to those of fish which died is lacking. To examine this question 25 chinook salmon were landed and for 16 of them series of blood samples were taken by caudal vein puncture during the post-exercise period. Individuals were tested from 2 to 9 times, depending upon their survival. Repeated handling undoubtedly contributed to fatigue and excessive mortality, hence this lot cannot be compared with other studies.

The results are summarized in Table V. Thirteen of the fish died, reflecting excessive handling. Two were considered very lively after 3 hours and were sampled and killed. Only one specimen survived repeated sampling and provided both a measure of high blood lactate 3 hours after exercise and low blood lactate almost 14 hours after hooking. The serial samples confirm that death was associated with attainment of high blood lactate concentration but indicate a wide range of variability in individuals. In 10 of the 13 cases, death occurred when blood lactate exceeded 200 mg%, and in 2 cases when it reached 174 mg%. In contrast, the 2 specimens that were lively after 3 hours of rest showed blood lactate of over 260 mg%, and blood lactate concentration of the survivor was at the same time 187 mg%. These observations demonstrate the variability among fish in the association between death and high blood lactate concentration following hyperactivity.

SUMMARY OF RESULTS

1. Troll-caught coho showed a typical delayed blood lactate response after hooking.
2. Blood lactate levels of coho feeding in the ocean increased at *least* 4-fold from pre-exercised levels in 2 hours.
3. For coho which died in the live box no significant decline in the blood lactate level was evident.
4. Mortality was estimated to lie in the range 0.336 to 0.522 at the 95% level of confidence. The empirical estimate is 0.437.
5. The mortality rate of coho reached a maximum in the second hour and then declined.
6. Mortality was substantially complete (97% of the definitive amount) by the end of 6 hours.
7. The recapture of tagged fish was not shown to be enhanced by holding in live boxes past the period of mortality.

TABLE V. Blood lactate (mg%) of 16 troll-caught ocean chinook which were sampled more than once.

Time period (*hours*)	Blood lactate concentration, *mg%*, for individual fish															
	No. 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
0– 0.5	51	101	72	32	46	29	51	49	85	181	49	45	91	74	59	36
0.5– 1.0	86 95	104	–	–	–	84	144	–	138	–	92	112	174 died	106	–	–
1.0– 1.5	105	138	142	–	–	130	–	87	199	204	died[a]	215 died		141	–	–
1.5– 2.0	153	144	177	–	–	–	186	–	219 died	died[a]				164	–	–
2.0– 3.0	159 169	177 196	177	111	–	178	224	262 died						–	–	–
3.0– 4.0	173	206	245	–	–	217 died	died[a]							187	261 killed	268 killed
4.0– 5.0	–	–	251 272 died	173 201 died	174 died									–		
5.0– 6.0	231 died	224 died												–		
6.0–10.0														–		
10.0–15.0														103 killed		

[a] Final blood sample not available.

8. A typical delayed blood lactate response to exercise was obtained for non-feeding adult coho in fresh water.
9. Degree of lactate response in freshwater was much less than in (2) above.
10. No deaths occurred among fish tested in fresh water.
11. It was noted (but not measured) that fish did not struggle as violently in fresh water as in salt water.
12. For ocean-caught chinook salmon which died, blood lactate was shown to have increased until death; while for a single survivor blood lactate reached a peak of 187 mg% at approximately the third hour and subsequently subsided to 103 mg% in the 14th hour.

DISCUSSION

The fact that blood lactate levels of coho increased following exertion on troll gear needs little discussion. Black (1957a) has described adequately the typical delayed response and this has been subsequently confirmed for several salmonids by Black (1957b,c) and Parker and Black (1959). Blood lactate levels of other Pacific salmon which died following hyperactivity were higher than blood lactate levels obtained from comparable living fish. The present study has confirmed this relationship for an additional species, the coho.

The fact that apparently uninjured fish died is not surprising. It is well known that severe muscular exertion may result in death of several species of animals. As early as 1938 Huntsman suggested that mortality in fish might result from severe muscular exertion. Subsequently several authors have reported instances of this occurring as outlined in the introduction to this paper and reviewed by Black (1958b). That significant numbers of troll-caught salmon have died in

TABLE VI. Comparison of delayed mortality observations on troll-caught salmon. (Detail of Fry's experiments are from a personal communication to the authors.)

Investigators	Species	Number in sample	Reported mortality estimate	Total time observed	0.95 binomial confidence interval
			%	*hours*	%
Milne and Ball (1954)	Coho	55	20	1–6	10–30
Milne and Ball (1958)	Coho	289	18	1+	13–22
Milne and Ball (1958)	Chinook	91	20	1+	12–28
D. H. Fry (*in litt.*)	Coho	88	38	16–24	28–47
D. H. Fry (*in litt.*)	Chinook	96	44	16–24	34–54
Parker and Black (1959)	Chinook	66	71	8	40–86
Present experiment	Coho	115	44	8	34–52

post-exercise activity has been reported several times. These observations are compared in Table VI. In each case significant mortality of fish captured by trolling occurred while being held aboard the fishing vessel in live tanks.

These experiments must be compared with caution. Those of Milne and Ball (1956, 1958) include only fish judged to be uninjured and fit for tagging,

as were fish used by Fry (Fry and Hughes, 1951) by Parker and Black (1959) and in the present experiment. Fry's experiments were carried past the term of maximum mortality rate, as were Parker and Black's and the present one. Milne and Ball liberated some fish prior to or during this period, either into a live pond or into the sea. All the experiments agree in the use of submature feeding fish in salt water. All investigators report that mortality is delayed and subsequently complete within 6 hours.

Mortality rate is closely correlated with blood lactate level. In Parker and Black's experiments with chinook and in the present experiment with coho the rate of mortality (*i*) is relatively low in the first hour, increases to a maximum in the second or third hour and becomes negligible by the end of 6 hours (Table III). This is the same type of delayed response described for blood lactate. Further, with a single exception in each of the above experiments, no fish died in which blood lactate levels were less than 125 mg% (see Fig. 1; also Parker and Black, 1959, Appendix). This is also true of Black's (1957c) sockeye experiment. Blood lactate levels above 125 mg% may, then, be considered as a danger zone for 3 species of Pacific salmon. This is not to say that when blood lactate levels rise above this point death will follow; rather, death *may* follow.

Several experimenters have subjected salmonids to hyperactivity but observed no ensuing mortality. Paulik, DeLacy and Stacy (1957) repeatedly subjected coho, and Paulik and DeLacy (1958) sockeye, to severe fatigue. Many of their test animals became so severely fatigued that equilibrium was lost, yet no significant mortality followed. In these experiments maturing adult fish were used in fresh water. Black (1957a,b) subjected rainbow trout and lake trout to hyperactivity without ensuing mortality. He noted a blood lactate response well above 125 mg% in these experiments. Jensen (1958) caught and released 2 and 3-year-old chinook salmon reared in salt water ponds. These fish were not fed 6 days prior to the experiment. Fish actively fought the lure for 1 to 2 minutes and were then easily netted and released. A small mortality of 2.0% occurred during the first week following treatment.

In our fresh water experiment, adult coho were treated in a manner essentially the same as fish on the troll gear. Lactate response was significant and typical. Quantitatively it was much less than for the feeding, sub-mature coho in the sea. Further, from subjective observations, fish ceased to struggle after less expenditure of effort than their salt water counterparts. Most significant: no deaths occurred. These observations appear to exclude psychosis from confinements, hook injury, abrasions of the mucous coat, etc., as primary factors of death. Death appears to be a condition brought about by severe fatigue of fish in a particular physiological state.

A greater recovery of tags was not realized by Fry and Hughes (1951) when only survivors held past the critical mortality period were released. These authors report a 1.63% recovery of tags from 123 chinook held overnight in live tanks after catching. A control group of 179 chinook gave 10.06% tag recovery. It is perhaps significant that tagging occurred at release, i.e. the survivors in the tanks were subjected to additional stresses of capture, tagging and releasing after the

recovery period, while the controls were tagged and released after capture, at a time when further handling could have had little effect in producing fatigue.

Milne and Ball (1958) obtained 27% recovery of 118 coho, tagged at capture, and held not less than one hour. In their earlier experiment (1956) 32% of the 28 tagged coho were subsequently recovered after being held in a floating live pond for more than 30 days. While no control lots were liberated, these recovery rates are much higher than previously reported experiments on troll tagging (Milne, 1957).

In the present experiment fish were tagged when captured and survivors released and compared with a control group. Recoveries have suggested less chance of survival for experimental fish than controls, and as in the case of Fry and Hughes (1951) the treatment during liberation is suspect. Survival from original fatigue is not the only consideration in these cases. A disoriented fish is easy prey to predators known to be present in the surface waters, i.e. mackerel shark (*Isurus nasus*) and northern seal lions (*Eumetopias jubata*). Further research is indicated along these lines. At present it is not possible to state methods by which mortality can be avoided; it can, however, be measured. It is suggested that fatigue is an indiscriminate stress acting in either a lethal manner or in an impairing manner (Brett, 1958) until full return to normal is achieved.

The mechanisms responsible for the differing susceptibility of salmon to effects of exercise in fresh and salt water may find explanation in the following arguments.

Most fish are chronically in oxygen distress because of low solubility of oxygen in water. Solubility is less than 10 mg/l for sea water in most cases (Sverdrup *et al.*, 1942), and less than 15 mg/l for fresh water in most cases (Welch, 1935). The active rate of oxygen uptake is restricted to a few multiples of the standard rate, i.e. approximately 4-fold (F. E. J. Fry, 1957). As in air-breathing animals, energy for activity in excess of the *active rate* (Fry, 1957) must be derived anaerobically, mainly by glycolysis. Job (1954) reported oxygen consumption at near the active rate for digestion of food alone, which indicates that any additional activities in a glutted stage of feeding must be accomplished anaerobically. The production of lactic acid and its diffusion into the blood must be considered as a regular physiological process for even moderate activity, and must be followed by rest. Loss of circulatory blood volume may result from severe muscular activity (Bainbridge, 1931). Black (1955) found a significant increase in blood hemoglobin following severe exercise in largemouth bass (*Micropterus salmoides*), and postulated an osmotic shift of water from the blood to the tissues in response to a greatly increased number of osmotically active particles present from hydrolysis of the large glycogen molecule. It is, of course, possible that increased blood hemoglobin results from introduction of stored erythrocytes into the circulating blood. If there is a significant increase in osmotically active particles within the muscle cells, it is possible that, in some situations, so much water may be drawn from the effective circulating blood that circulatory shock may ensue. Further, upon diffusion of hydrogen ions and (or) lactate ions into the blood, the blood fluid may become severely hypertonic to the erythrocytes—

which may explain the observations of von Buddenbrock (1938) that the red blood cells appeared to be collapsed and misshapen when blood lactate levels were high. This condition could further aggravate the situation by reducing oxygen transport ability of the circulating blood. Fish in sea water obtain water from either oxidation of food or by drinking sea water and excreting the salts, a process which involves cellular work (see V. S. Black 1957). Thus an osmotic imbalance caused by excessive production of lactate ions could lead to a distressed condition of suffocation.

Sub-adult Pacific salmon, susceptible to trolling, are in a feeding stage. Large quantities of food are consumed, fat is being stored and protein synthesized. Carbohydrate, available as liver glycogen, blood glucose and muscle glycogen, is readily available for quick energy (unpublished observations of E. C. Black). As maturity is approached these fish cease feeding and enter fresh water. Energy for ascending streams and for the spawning act is available only through use of stored fat and catabolism of non-essential protein (Green, 1926; Hoar, 1957; Black, 1958a). This material is presumably not available for rapid consumption and thus the rate of supply can restrict the action of the fish in its response to stimuli. If feeding fish are starved for periods prior to exercise, the above mentioned sources of fat and protein must be drawn upon for energy. Thus, coho salmon did not struggle as violently in fresh water, not because of any basic difference in stimulus-response reaction, but because of limited stores of readily available energy. Jensen's experiment is consistent with this hypothesis. His fish were not fed for 6 days prior to the test. (In addition they may have been considerably adapted to handling). The cessation of feeding also implies that more oxygen will be available for respiration associated with activity. From these arguments, the lack of mortality of fish in fresh water may be explained, as well as giving a mechanism for death following hyperactivity of feeding salmon in sea water.

It would appear that cessation of feeding by Pacific salmon, coincident with approaching maturity and entrance into fresh water, may be a contributing factor to the ability of the fish to migrate extensive distances up stream. If large amounts of muscle glycogen were available there would be no check on the rate of energy expenditure and at rapids or other obstructions salmon might become disoriented from sustained severe activity. The slower mobilization of stored fats and non-essential proteins may act as an effective "pacer", preventing disorientation following fatigue, a condition which might lead to passive displacement down stream, thus net loss and needless expenditure of energy. Lack of feeding is thus viewed as a protective mechanism of survival value for Pacific salmon.

CONCLUSIONS

1. Chinook and coho salmon caught by trolling undergo hyperactivity.
2. This often leads to a distressed condition which is delayed and the severity of which cannot be predicted for any individual at the time of capture.

3. The distressed condition may advance beyond the ability to respond to stimuli or to recover orientation and terminate in death.
4. Death resulting from capture by troll has been observed to be of significant magnitude. For coho, mortality lies between 34% and 52%; for chinook, between 40% and 86%.
5. Mortality rate and blood lactate levels are closely correlated in relation to post-exercise time.
6. For fish which died, blood lactate rose until death. Survival occurred either when blood lactate did not reach critical levels (above 125 mg%) or reached a critical level and then subsided.
7. No remedy is suggested for delayed mortality from fatigue of troll caught salmon. It is important that it be assessed in tagging programs.
8. Holding salmon for tagging past the period of mortality did not improve tag recovery. It is suggested that the manner of releasing is responsible for additional indiscriminant stress acting in both a lethal and impairing manner.
9. This observation suggests that the largest *number* of returns can be gained by tagging all fish available and releasing immediately. Subsequent mortality can be assessed by holding lots on board.
10. Adult coho salmon did not appear susceptible to fatigue to a lethal degree in fresh water. This has been postulated as due to cessation of feeding and to have adaptive significance for survival.

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APPENDIX: A METHOD OF COMPUTING THE VARIANCE OF COMBINED PROBABILITY ESTIMATES

Mortality of fish is studied and a series of consecutive observations are obtained. Each estimate of mortality may or may not be based on samples of identical individuals, i.e. each sample may be drawn independently from the population. It is desired to estimate the probability Q that a fish will die prior to or during a time period t and to set up confidence intervals for these probabilities. This procedure would not, of course, be needed if a constant instantaneous mortality obtained throughout the time period. The assumption of random selection must be valid.

The following notation is used:

$\hat{p}_t$ estimates the probability p_t that a fish living at time t survives until $t + 1$.

$\hat{q}_t$ estimates q_t, the probability that a fish living at time period t dies before time period $t + 1$; $q_t = 1 - p_t$.

x_t = number of fish alive at time t that survive until time $t + 1$.

y_t = number of fish alive at time t that die before time $t + 1$.

n_t = number of fish alive and in the experiment at time t, $n_t = x_t + y_t$; $p_t = x_t/n_t$.

$\hat{P}_t$ = estimates the probability P_t that a fish lives until time $t + 1$,

$\hat{Q}_t$ = estimates the probability Q_t that a fish dies prior to time $t + 1$. NOTE: it may also die prior to time t, $t - 1$, etc.

The qualification has been given that n_t may or may not equal x_{t-1}.

Now $P_t = p_0 p_1 \ldots p_{t-1} p_t$, or:

$$P_{t-k} = \prod_{t=0}^{k} p_t \tag{1}$$

and $Q_t \neq q_0 q_1 \ldots q_{t-1} q_t$ because a joint probability of death cannot occur, but:

$$Q_t = 1 - P_t \tag{2}$$

It can be estimated from this relationship or by use of the logarithmic form:

$$Q_t = 1 - e^{-(\text{coln}p_0 + \text{coln}p_1 + \ldots + \text{coln}p_{t-1} + \text{coln}p_t)}$$

or

$$Q_t = 1 - e^{-(i_1 + i_2 + \ldots + i_{t-1} + i_t)}$$

where $i_t = \text{coln}\hat{p}_t$ = instantaneous mortality rate (Ricker, 1945). In any case Q_t is always estimated from $\hat{P}_t$ or its components.

Variance of p_t is estimated (Snedecor, 1950) by:

$$s^2_{P_t} = \frac{\hat{p}_t \hat{q}_t}{n_t}$$

The variance of $\hat{P}_t$ cannot be sums or products of variances of $\hat{p}_t$'s for resulting variances would rapidly diverge and lose meaning. The variance of $\ln\hat{p}_t$ (or $\text{coln}\ \hat{p}_t$) may be approximated (Deming, 1943, p. 45), by:

$$s^2_{\ln p_t} \approx \frac{s^2_{\hat{p}_t}}{\hat{p}_t^2}$$

These variances are additive and thus:

$$s^2_{\ln\hat{P}_{t-k}} = \sum_{t=0}^{k} s^2_{\ln\hat{p}_t} \tag{3}$$

Confidence intervals of Q_t can now be set by the relationship:

$$1 - \hat{P}_t e^{(t_{.05} s_{\ln\hat{p}_t})} \leqq Q_t \leqq 1 - \hat{P}_t e^{-(t_{.05} s_{\ln\hat{p}_t})} \tag{4}$$

The resulting confidence limits are advantageous as they tend to the unequal limits of the Poisson distribution as values of $P \to 0$ or 1. A schedule of calculations is presented in Table A. Mortality observations were grouped in time periods of one hour and calculations are carried out in Table B.

TABLE A. Schedule for calculation of standard deviation of $\log_e$ survival probability.

	x	y	n	$\hat{p}$	$\hat{P}$	$s^2_{\ln\hat{p}}$	$s_{\ln\hat{P}}$
0	x_0	y_0	n_0	x_0/n_0	$\hat{p}_0$	y_0/x_0n_0	$(s^2_{\ln\hat{P}_0})^{1/2}$
1	x_1	y_1	n_1	x_1/n_1	$\hat{P}_0\hat{p}_1$	y_1/x_1n_1	$(s^2_{\ln\hat{P}_0} + s^2_{\ln\hat{p}_1})^{1/2}$
2	x_2	y_2	n_2	x_2/n_2	$\hat{P}_1\hat{p}_2$	y_2/x_2n_2	$(s^2_{\ln\hat{P}_1} + s^2_{\ln\hat{p}_2})^{1/2}$
..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..
$t-1$	x_{t-1}	y_{t-1}	n_{t-1}	x_{t-1}/n_{t-1}	$\hat{P}_{t-2}\hat{p}_{t-1}$	$y_{t-1}/x_{t-1}n_{t-1}$	$(s^2_{\ln\hat{P}_{t-2}} + s^2_{\ln\hat{p}_{t-1}})^{1/2}$
t	x_t	y_t	n_t	x_t/n_t	$\hat{P}_{t-1}\hat{p}_t$	y_t/x_tn_t	$(s^2_{\ln\hat{P}_{t-1}} + s^2_{\ln\hat{p}_t})^{1/2}$

TABLE B. Schedule of calculation of mortality for ocean coho (see text and Table A for notation).

t	x	y	n	$\hat{p}$	$\hat{P}$	$s^2_{\ln\hat{p}}$	$s_{\ln\hat{P}}$	$\underline{Q}$	$\hat{Q}$	$\bar{Q}$	i
0	110	5	115	0.9565	0.9565	.000395	.01987	0.006	0.044	0.080	0.044
1	89	21	110	0.8091	0.7739	.002145	.05040	0.146	0.226	0.299	0.212
2	75	14	89	0.8427	0.6522	.002097	.06810	0.255	0.348	0.429	0.171
3	72	1	73	0.9863	0.6433	.000190	.06948	0.263	0.357	0.438	0.038
4	69	3	72	0.9583	0.6165	.000604	.07370	0.288	0.384	0.474	0.043
5	59	4	63	0.9365	0.5774	.001076	.08067	0.330	0.423	0.507	0.066
6	52	0	52	1.0000	"	...	"	"	"	"	0
7	47	0	47	"	"	...	"	"	"	"	0
8	40	1	41	0.9756	0.5633	.000610	.08436	0.336	0.437	0.522	0.025

Orange-red Flesh in Cod and Haddock[1]

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ABSTRACT

Only rarely is Atlantic cod found with orange-red coloured skin and flesh. Astaxanthin and zeaxanthin, in the proportion of 2:1, were found to be responsible for the pigmentation of the flesh of such a specimen. Zeaxanthin was the only pigment detected in the flesh of a similarly pigmented haddock.

The pigments of most fishes are localized in the skin, and in only a few species, such as salmon, is the muscle tissue pigmented. The colour of salmon flesh is due mainly to astaxanthin (Bailey, 1937; Kanemitsu and Aoe, 1958a), a pigment found in most crustacea. Occasionally, however, individuals of species which are normally unpigmented are found to have coloured flesh. Baalsrud (1956) examined a cod which had red-coloured flesh. He extracted the pigments with acetone and from the absorption spectrum (see Fig. 1) concluded that the coloration was due to the presence of astaxanthin (esterified). Templeman and Sandeman (1958) have reported a redfish (*Sebastes marinus* L.), the fillets of which were coloured salmon-pink. They also referred to the occurrence of cod and haddock with salmon-pink flesh.

During recent years four or five cod (*Gadus callarias* L.) with pigmented flesh have been examined in this laboratory. In June of 1958, a specimen 25 inches (63.5 cm) long was received which had been caught off Devil's Island in the mouth of Halifax Harbour. This cod seemed more intensely pigmented than previous ones. The entire fish, including head, fins, and the lining of the visceral cavity, had pronounced orange-red pigmentation. The orange-red colour was also present throughout the muscle tissue. The moisture and lipid contents of the flesh were normal, 82 and 0.8%, respectively (moisture determined by drying to constant weight at 105°C; lipid determined according to Bligh and Dyer [1959]).

Present knowledge regarding the pigments responsible for the coloration in these unusual specimens is based on absorption spectra only. It was therefore considered that a somewhat more detailed study of the pigments of this unusual cod would be desirable.

The absorption spectrum of an acetone extract of the muscle tissue agreed with those of similar extracts prepared by Baalsrud (1956) and by Templeman and Sandeman (1958), (Fig. 1), thus indicating the presence of astaxanthin. When a portion of the acetone extract was evaporated to dryness under nitrogen and the pigments partitioned between petroleum ether (boiling range 30–60°C) and 90% (v/v) aqueous methanol, almost all of the orange-red colour appeared in the methanol layer. This indicated that the astaxanthin was primarily present in the

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unesterified form (cf, Goodwin and Srisukh, 1949), which is in contrast to Baalsrud's finding.

Chromatographic separation of the pigments was carried out as described by Goodwin and Srisukh (1949). The pigments, in petroleum ether, were applied to the top of a column of weakened alumina. Elution with petroleum ether removed only a trace of yellow colour. Subsequent elution with 95% ethanol

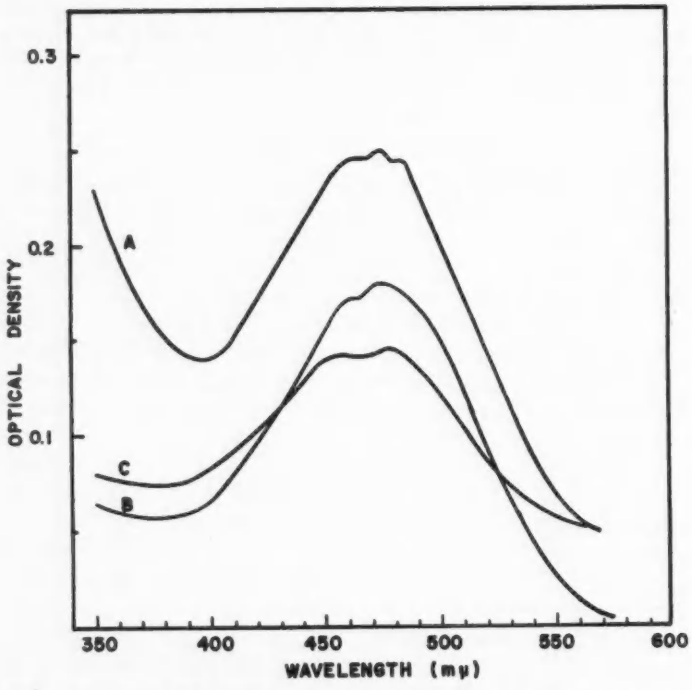

FIG. 1. Absorption spectra of acetone extracts of muscle tissue (100 ml acetone per 21 g tissue; optical densities calculated or measured to a light-path of 1 cm).
A — Redfish, from Templeman and Sandeman (1958).
B — Cod, from Baalsrud (1956).
C — Pigmented cod.

removed an orange band (Pigment I). The bulk of the pigment on the column (Pigment II) was eluted with 2% (v/v) glacial acetic acid in 95% ethanol; this is characteristic of astaxanthin (cf. Goodwin and Srisukh, 1949). A pink band (Pigment III) remaining at the top of the column was removed with 2.5% (w/v) KOH in 95% ethanol. This is a characteristic property of astacin (cf. Goodwin and Srisukh, 1949) which is formed from astaxanthin by oxidation. After the KOH–ethanol eluate had been neutralized with acetic acid, the three pigment-containing eluates were evaporated to dryness under nitrogen. Each residue was

dissolved in a small volume of methanol and the absorption spectrum was determined.

These findings and the absorption spectra given in Fig. 2 led to the conclusion that Pigments II and III were astaxanthin and astacin. Astacin, as such, has not

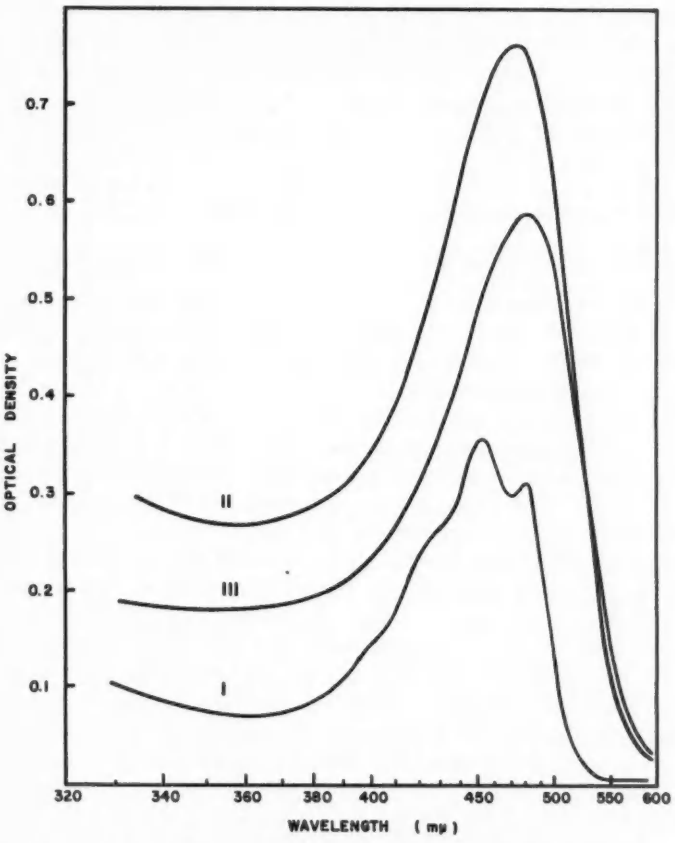

FIG. 2. Absorption spectra of coloured fractions separated from pigmented cod extract by column chromatography.
I — (Zeaxanthin); λ max. 452 and 479 mμ.
II — (Astaxanthin); λ max. 469 mμ.
III — (Astacin); λ max. 479 mμ.

been found in nature and that which was isolated from the extract probably originated from astaxanthin.

Pigment I was initially thought to be esterified astaxanthin. The absorption spectrum (Fig. 2), however, was not that of esterified astaxanthin but was practically identical to that of either β-carotene or zeaxanthin (cf. Karrer and Jucker,

1950). When partitioned between petroleum ether and 90% methanol the pigment accumulated in the methanol layer, a property of zeaxanthin which distinguishes it from β-carotene. This evidence indicated that Pigment I was zeaxanthin.

The above pigments all have similar extinction coefficients and consequently the relative amounts present in the tissue could be calculated. For the purposes of these calculations astacin was considered as astaxanthin. The results indicated that approximately two-thirds of the colour was due to astaxanthin and one-third due to zeaxanthin.

An estimation of pigment concentration in the flesh of the cod indicated that there was less pigmentation than in salmon. Kanemitsu and Aoe (1958b) report astaxanthin levels of about 3.3 and 0.5 mg% in sockeye and spring salmon (*Oncorhynchus nerka* and *O. tschawytscha*) respectively. Utilizing their extinction coefficient for astaxanthin in acetone ($E^{1\%}_{1cm} = 2{,}200$, at 478 mμ), and data in Fig. 1, it was estimated that this cod contained about 0.3 mg pigment per 100 g flesh. The redfish of Templeman and Sandeman (1958) having a pigment concentration of about 0.5 mg% was more comparable to salmon. As a matter of interest, the pigment content of the skin of a normal redfish was 1.8 mg%.

Thus the orange-red pigmentation of the flesh of this atypical cod appeared to be due to the presence of astaxanthin and zeaxanthin in the proportion of 2:1. The astaxanthin occurred in the free form rather than esterified, as reported by Baalsrud (1956). This is the first reported occurrence of such a large proportion of zeaxanthin in fish flesh (see Goodwin, 1951).

During the preparation of this report a haddock (*Melanogrammus aeglefinus* L.) was received which appeared to be atypical only in that the fillets were slightly pink in colour. The moisture and lipid contents were 80 and 0.7% respectively. The pigment concentration was approximately one-tenth of that of the cod described above. The results obtained when the extracted pigments were subjected to chromatography were quite unexpected. Astaxanthin and astacin were not detected and the coloration appeared to be due entirely to zeaxanthin. The absorption spectrum of the isolated pigment was identical to that of Pigment I in Fig. 2.

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The Annual Oceanographic Cycle at Igloolik in the Canadian Arctic. 1. The Zooplankton and Physical and Chemical Observations[1]

CALANUS SERIES, No. 20

BY E. H. GRAINGER

Fisheries Research Board of Canada, Arctic Unit, Montreal, P.Q.

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ABSTRACT

Materials used were collected September 1955 to September 1956 near Igloolik, northwest Foxe Basin, in the Canadian arctic. A single station, about one mile from shore and 52 m deep, was occupied 27 times during the year. It is in a region of net flow of arctic water from Fury and Hecla Strait, whose strong current probably brings ever-changing hydrographic conditions and plankton populations to the station area. Sea ice formed in early

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November, and had thickened to about 152 cm by early May. Melting then began and continued until the station was free of fast ice soon after mid-July. Water temperatures varied only 3.55°C at all depths during the year, and only 0.07° from November until May. The coldest record was –1.75° at 50 m in April and May, the warmest 1.80° at the surface in early September. Salinities varied from a maximum of 32.59‰ in early May to less than 1.68‰ at the surface in mid-July. A thin layer of brackish water, probably not exceeding 2 m in depth, was developed at the surface during the ice-melting period from late June until early August. Dissolved oxygen content varied from 9.52 ml/l in early July to 4.08 ml/l in early September. The maximum saturation recorded was 110.3% at 10 m on July 15. Dissolved inorganic phosphate rose from near zero in February to a maximum of 1.5 μg-at/l in mid-June, then declined until autumn.

Zooplankton volume (from the coarse net) was greatest in late September (4.85 ml per 50-m haul), least in mid-April (0.15 ml). Among identifiable material, copepods were volumetically the largest group. Twenty-eight species were identified, the most numerous forms being copepods (*Pseudocalanus minutus, Calanus finmarchicus, C. hyperboreus, Oithona similis*), chaetognaths (*Sagitta elegans*), cirriped larvae, medusae (*Halitholus cirratus*) and larvaceans (*Fritillaria borealis*). Several of the more abundant species provide life-history information. All the plankton species had previously been collected in the arctic, and all are circumpolar (one possible exception).

Propagation times of primarily herbivorous plankters coincide with the abundance of their phytoplankton food, and the numerical cycle of these individuals during the year shows a restricted period of maximum numbers during the time of reproduction (summer) followed by gradual decline until late winter. In contrast, the primarily carnivorous plankters show relatively slight numerical variation throughout the year, and no concentrated period of reproduction. These species reproduce at various times of the year, many of them during winter. A rough estimate of the Igloolik yearly mean standing crop of zooplankton (without correction for straining efficiency of the No. 6xxx net) is 0.10 ml/m^3 or 5.2 ml/m^2 of surface area; the maximum observed was 0.50 ml/m^3. Another arctic coastal locality, in Greenland, had similar figures; coastal boreal stations have mean crops 4 to 8 times as great (volume basis) or 2 to 9 times as great (surface area basis).

INTRODUCTION

DURING THE PERIOD September 1955 to September 1956, regular oceanographic observations and collections were made by the author near Igloolik, at the eastern end of Fury and Hecla Strait, in the Canadian arctic (Fig. 1). Previous to this time, no comparable year-round study had been carried out in the waters of northern Canada, marine investigations (with the notable exception of those of Ellis (1956, and unpublished)) having been confined almost entirely to the summer, open-water periods. The M/V *Calanus*, arctic vessel of the Fisheries Research Board of Canada, was situated at Igloolik from the summer of 1955 until the summer of 1956, and was used as the base of operations for the investigations described below.

Since the winter of 1822–1823, when Sir Edward Parry froze the ships *Fury* and *Hecla* in the sea ice near the mouth of Turton Bay (Parry, 1824; Lyon, 1824), few expeditions have visited northern Foxe Basin, and until 1955 none had as its principal object oceanographic investigations. In the same year as the study described here was begun, H.M.C.S. *Labrador* carried out an oceanographic cruise in Foxe Basin (Campbell and Collin, 1956), and in 1956 the *Labrador* returned to conclude investigations in the same region (Campbell, 1958). An account of

exploration in Foxe Basin is given by Fraser (1953), brief summaries of the physical geography of northern Foxe Basin by Fraser, and of the physical oceanography by Campbell and Collin (1956).

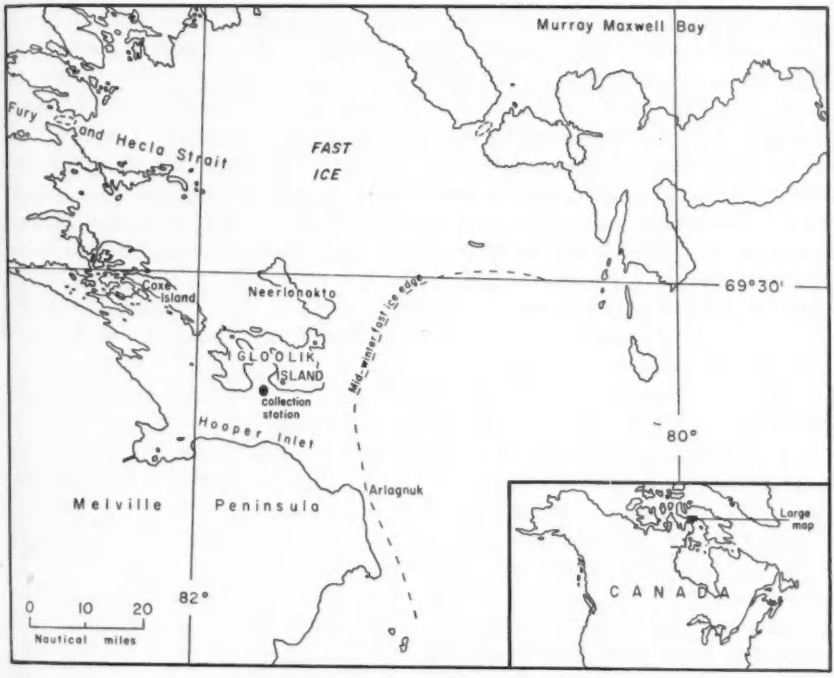

FIG. 1. Northwestern Foxe Basin and the eastern end of Fury and Hecla Strait. The area represented on the large map is shown in the inset.

This paper deals with the physical and chemical observations made and the zooplankton collected. A second paper, on the Igloolik phytoplankton, is at present being prepared by Adam Bursa, and will be published as a part of the *Calanus* series at a later date.

METHODS

The site chosen for a year-long series of collections and observations was at the mouth of Turton Bay (69° 20.5′ N, 81° 43.5′ W), in 50 m of water. Operations were carried out from boats during the open-water periods of September to October 1955, and August to September 1956, and through holes cut in the sea ice during the remainder of the year. Collections were made at depths of 0, 10, 25 and 50 m. A Nansen bottle equipped with a reversing thermometer was used

for salinity, oxygen, phosphate and microplankton collections, and for temperature readings. Salinity samples were stored, unfrozen, for later titration by the Atlantic Oceanographic Group, St. Andrews, N.B. Oxygen and phosphate samples were analysed in the field, the former by the Winkler method, the latter by a modification of the Déniges colorimetric method. Oxygen saturation values were computed from the tables of Fox (1907). Microplankton collections, of about 150 ml, were preserved and were brought to the laboratory for examination under the Utermöhl inverted microscope (Bursa, MS). Plankton was also collected with nets of No. 0xx, No. 6xxx and No. 20 silk, the two larger meshes fitted to half-metre diameter rings, the smaller an Apstein net (20 cm ring diameter). The three nets were used at nearly all occupations of the station, and for most collections each was used for three successive vertical hauls, the collection being removed after each haul. All net hauls were made from 50 m to the surface, and a constant hauling speed of about 70 seconds per 50-m vertical haul was maintained, the nets being raised by means of a hand-operated winch. The water column through which the 0xx and 6xxx nets were hauled was therefore 9.8 m^3, which can be taken as the upper limit of the volume of water strained by these nets. The station was occupied 27 times during the year.

In the laboratory, hauls from all three nets were used in analysis of the zooplankton. The No. 0xx (aperture 0.569 mm) hauls, with a negligible amount of phytoplankton in only a few early summer collections, were used for zooplankton volume assessment. Entire contents were sorted into taxonomic groups, and the contents of each group were spread thinly on a piece of fine nylon which was pressed over the surface of absorbent paper. The paper was renewed until no signs of moistening appeared, then the plankton was transferred from the silk to a graduated cylinder, which could be read satisfactorily to 0.05 ml and the volume was determined by water displacement. While most collections represented three consecutive 50-m hauls, some (taken chiefly in August and September) were from only a single haul, while a few others were from two hauls. All results are expressed in terms of one haul, by dividing the yields of 3-haul and 2-haul collections by the appropriate numbers. For qualitative assessment of the No. 0xx hauls, entire samples were analysed, and all individuals were identified and counted. Counts are expressed in terms of single hauls, which could have strained up to 9.8 m^3 of water, that lying under 2.0 m^2 of sea surface.

The No. 6xxx (aperture 0.239 mm) hauls were sub-sampled, between 5% and 20% of the collections being taken for analysis. Only species inadequately represented in the larger mesh No. 0xx net hauls were considered. As with the No. 0xx plankton, all counts are expressed as per single haul. Much of the content of the No. 6xxx net hauls was phytoplankton.

The No. 20 (aperture 0.076 mm) net hauls could not be studied quantitatively because of improper handling in the laboratory. Consequently, these samples were examined only for forms not found in the two larger nets, and specimens were identified and recorded only as being either present or not found on the various collection dates. The No. 20 net hauls supplemented the bottle collections of microplankton in the study of the phytoplankton (Bursa, MS).

Zooplankton organisms were examined under a 6- to 80-power binocular microscope, and measurements were made using an ocular micrometer. Measurements are expressed, for the most part, in millimetres, except where large numbers of copepod lengths are given in micrometer units, each of which equals 0.063 mm. All units of measurement are identified in the text. All copepod measurements are of cephalothoracic length.

AIR TEMPERATURE AND SUNLIGHT

The mean air temperature in January in the Igloolik region has been given as about –30°F (–34°C), in July as +40° to +45°F (+4° to +7°C) (Rae, 1951). The period of winter darkness lasts from about November 25 until near the middle of January, during which time of about 50 days direct sunlight is totally absent. Twenty-four hours of direct sunlight per day begins in mid-May and lasts until near the end of July, a period of about 75 days. Times of approximately equal periods of direct sunlight and darkness are in early October and early March.

GENERAL HYDROGRAPHIC OBSERVATIONS

The general pattern of water circulation among the islands north of the Canadian mainland is from west to east and from north to south (Dunbar, 1951; Bailey, 1957). A part of this general movement of arctic water is shown as passing eastward through Fury and Hecla Strait, and southward along the east shore of Melville Peninsula, on the west side of Foxe Basin (Parry, 1824); Dunbar, 1951; Campbell and Collin, 1956). No precise current measurements were made in the Igloolik vicinity during 1955 and 1956, but observations at various points around the island, made mostly on floating ice, suggested a dominant west to east flow through Hooper Inlet, and a north to south flow off the west and east coasts of Igloolik Island. The influence of arctic water from the northwest would therefore be expected to be dominant at Igloolik. The magnitude of this transport within the constriction of Fury and Hecla Strait appears to be considerable, an eastward surface current of 3 to 4 knots having been reported by Parry (1824). Such a flow passing Igloolik Island may be expected to have considerable influence upon oceanographic conditions at the collecting station, with variations in horizontal transport and vertical movements causing fluctuations in the composition of the plankton and in the physical and chemical properties of the samples.

SEA ICE

Thin films of ice formed several times over the surface of Turton Bay during early October 1955, when water temperatures ranged from about –0.5° to –1.0°C at the surface, and air temperatures varied from about –1°C (30°F) to –9°C (15°F). Constantly broken by winds, the ice cover did not achieve winter permanence until October 21, a state maintained until the end of July. While this ice formation occurred within the comparative shelter of Turton Bay, the more

exposed waters of Hooper Inlet and beyond remained open for a longer time. On October 27 the ice within Turton Bay (2½ miles from the collecting station) had thickened to about 10 cm, but the area of solid land-fast ice reached only to within the mouth of Turton Bay (about ½ mile from the station), where a temporary ice edge remained for about one week. During late October ice formed then broke up in Hooper Inlet, and it was not until early November that winter ice became fixed over the station point. By November 12, a solid ice cover had formed across Hooper Inlet, and the ice edge had taken up a position facing open Foxe Basin water, along a north-south line east of Turton Bay. During this time the ice had formed over the sea area to the west of Igloolik Island, to the north between Igloolik and Neerlonakto, and off the east coast as a narrow band parallel to the shore. Farther afield, the various bays of northern Foxe Basin had been covered, and the slow encroachment of the fast ice upon the open water area of the Basin had begun. Not until near the end of the year, however, did the ice edge reach its maximum distance from the shores, and take up the mean winter-time position. This position did not remain rigidly fixed. Pack ice, moved about constantly by winds and currents, caused minor and usually short-term changes in the position of the ice edge. Within the limits of these variations, however, the ice edge remained more or less as shown in Fig. 1 from January until June, about 10 miles east of the collection station.

During June the first sustained melting began (short-term melting having occurred since mid-May), and areas of rotting ice appeared over the entire fast ice surface. By the first of July the fast ice had cleared away from the Melville Peninsula coast near Arlagnuk, and open water reached nearly to the southeast point of Igloolik Island, with the ice edge running approximately along a line joining the two points. By the middle of July the edge had moved into Hooper Inlet, about half way between southeastern Igloolik Island and Turton Bay, by July 23 almost to Turton Bay, and by the end of July to within Turton Bay. In early August only small patches of fast ice along with a few off-shore grounded floes remained round Igloolik.

Data on ice thickness at the collecting station are given in Table I and Fig. 2(a). From the time of initial freezing, about the first of November, the ice thickness increased until early May, when it measured about 152 cm. Melting, beginning in early May, slowly decreased the thickness and rotted the ice cover until, shortly after the middle of July, the station was free of fast ice. Only infrequent and brief drifts of pack ice covered the station point until the last occupation on September 13.

Until the end of December the snow cover was small, only a few centimetres in thickness, and evenly distributed over the fast ice. From early January until at least the time of first melting (May) the average snow thickness was much greater, and varied considerably, due to wind drift, from a few centimetres to more than a metre. Even after melting began, large snowfalls in early June caused, at least temporarily, thick covers of snow over the ice. Not until the end of June had the snow largely disappeared, leaving transparent pools and uncovered ice on the surface.

WATER TEMPERATURE

The yearly water temperature cycle at Igloolik is shown in Fig. 2(b) and Table I. Temperatures at all depths fell from September until November. From November until May a variation of only 0.07°C was recorded throughout the water column. The coldest water (−1.75°) was found at 50 m during all of April and

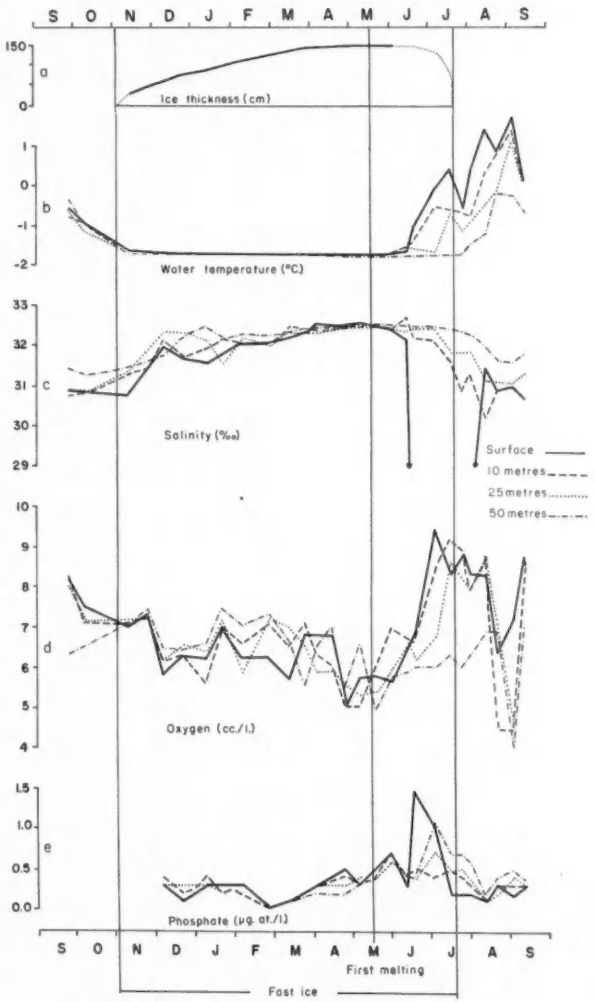

FIG. 2. The annual cycles of (a) ice thickness, (b) water temperature, (c) salinity, (d) dissolved oxygen, and (e) dissolved inorganic phosphate, from September 1955 until September 1956.

TABLE I. Date, time (eastern standard), air temperature, ice thickness, water temperature, salinity, dissolved oxygen and dissolved inorganic phosphate data from Igloolik, 1955–1956. Starting times only are given for station occupations. Only one reversing bottle was used, thus time lapses of up to 20 minutes occurred between successive samplings, except for the period August 11 to September 13, 1956, when all depths were sampled simultaneously.

Date	Time	Air temp.	Ice	Depth	Temp.	Salinity	O_2	O_2	PO_4-P
day/ month		°C	cm	m	°C	‰	ml/l	% sat'n	µg-at/l
25/9	1525	–1	...	0	–0.50	30.72	8.16	96.8	...
				10	–0.70	30.72	8.23	97.2	...
				25	–0.59	30.81	8.01	94.9	...
				47	–0.44	31.55	6.30	75.4	...
5/10	1430	–3	...	0	–0.99	30.82	7.47	87.2	...
				10	–1.00	30.82	7.07	82.6	...
				25	–1.05	30.81	7.15	83.6	...
				50	–1.00	31.22	6.52	76.6	...
10/11	1345	–10	23	0	–1.65	30.75	6.98	80.5	...
				10	–1.70	31.31	7.05	81.5	...
				25	–1.71	31.36	7.15	82.7	...
				50	–1.71	31.36	7.07	81.7	...
25/11	1258	–30	45	0	–1.70	31.42	7.35	85.1	...
				10	–1.68	31.44	7.25	83.9	...
				25	–1.70	...	7.15	...	...
				50	–1.70	31.56	7.43	86.1	...
7/12	1145	–23	59	0	–1.68	32.03	5.91	68.7	0.3
				10	–1.68	32.12	6.16	71.7	0.4
				25	–1.68	32.36	6.22	72.5	0.3
				50	–1.68	31.78	6.50	75.4	0.4
22/12	1158	–22	76	0	–1.70	31.71	6.30	73.0	0.1
				10	–1.70	31.71	6.28	72.8	0.2
				25	–1.71	32.34	6.52	76.0	0.3
				50	–1.71	32.20	6.46	75.2	0.2
9/1	1230	–17	86	0	–1.70	31.58	6.22	72.1	0.3
				10	–1.70	31.91	5.61	65.2	0.3
				25	–1.70	32.16	6.40	74.5	0.3
				50	–1.72	32.48	6.64	77.5	0.4
23/1	1400	–32	98	0	–1.70	31.85	7.03	81.5	0.3
				10	–1.70	32.20	7.09	82.5	0.3
				25	–1.70	31.53	7.23	83.6	0.2
				50	–1.70	32.20	7.51	86.5	0.2
7/2	1115	–41	112	0	–1.70	32.07	6.21	72.2	0.3
				10	–1.70	32.10	6.63	77.1	0.2
				25	–1.70	32.20	5.77	67.2	0.3
				50	–1.70	32.30	7.10	82.8	0.3
27/2	1215	–17	125	0	–1.72	32.09	6.26	72.8	0.0
				10	–1.72	32.10	7.13	82.9	0.0
				25	–1.72	32.01	7.27	84.4	0.0
				50	–1.73	32.25	7.37	85.8	0.0
13/3	1500	–42	134	0	–1.71	...	5.71	...	0.1
				10	–1.71	32.45	6.56	76.5	0.1
				25	–1.72	32.38	6.97	81.2	0.1
				50	–1.72	32.38	6.69	78.0	0.1

TABLE I: *continued*

Date	Time	Air temp.	Ice	Depth	Temp.	Salinity	O_2	O_2	PO_4-P
day/ month		°C	cm	m	°C	‰	ml/l	% sat'n	µg-at/l
26/3	1320	–23	140	0	–1.71	32.38	6.87	80.1	...
				10	–1.71	32.38	7.15	83.3	...
				25	–1.71	32.39	6.53	76.1	...
				50	–1.72	32.45	5.58	65.1	...
4/4	1545	–9	143	0	–1.70	32.50	6.83	79.7	0.3
				10	–1.72	32.41	6.40	74.6	0.3
				25	–1.73	32.38	5.91	68.8	0.3
				50	–1.75	32.47	6.60	76.9	0.2
14/4	1515	–4	147	0	–1.70	32.47	6.83	79.7	...
				10	–1.72	32.45	6.07	70.8	...
				25	–1.73	32.45	6.69	77.8	...
				50	–1.75	32.47	7.04	82.0	...
26/4	1325	–14	150	0	–1.72	32.45	5.07	59.2	0.5
				10	–1.72	32.45	5.07	59.2	0.4
				25	–1.73	32.47	5.45	63.5	0.3
				50	–1.75	32.48	5.34	62.2	0.2
5/5	1255	–11	152	0	–1.72	32.59	5.75	67.1	0.3
				10	–1.72	32.48	5.09	59.4	0.3
				25	–1.73	32.50	5.32	62.0	0.4
				50	–1.75	32.48	6.60	76.9	0.3
19/5	1355	–6	152	0	–1.67	32.48	5.86	68.5	0.5
				10	–1.71	32.48	...	...	0.4
				25	–1.71	32.48	5.47	63.8	0.4
				50	–1.71	32.52	4.94	57.6	0.4
30/5	1430	–6	...	0	–1.70	32.45	5.68	66.3	0.7
				10	–1.70	32.41	7.07	82.4	0.7
				25	–1.71	32.41	6.05	70.4	0.6
				50	–1.72	32.52	5.83	68.0	0.6
13/6	1200	–1	...	0	–1.60	32.18	6.53	76.2	0.3
				10	–1.51	32.72	6.77	79.5	0.4
				25	–1.53	32.38	6.70	78.4	0.4
				50	–1.71	32.52	5.97	69.7	0.4
19/6	1615	4	...	0	–0.96	27.01	6.84	78.0	1.5
				10	–1.32	32.23	6.76	79.4	0.5
				25	–1.60	32.45	6.26	73.2	0.5
				50	–1.71	32.52	6.09	71.1	0.4
2/7	2325	0	...	0	–0.09	1.68	9.52	91.0	1.0
				10	–0.43	32.16	8.50	102.3	0.4
				25	–1.68	32.45	6.84	79.8	0.7
				50	–1.72	32.52	6.09	71.1	1.1
15/7	1625	7	...	0	0.50	<1.68	8.32	...	0.2
				10	–0.50	31.60	9.23	110.3	0.5
				25	–0.63	31.87	8.69	103.7	0.5
				50	–1.63	32.47	6.31	73.7	0.7
25/7	2245	1	...	0	–0.50	10.41	8.92	91.4	0.2
				10	–0.60	30.82	8.79	104.2	0.4
				25	–1.05	31.91	...	...	0.5
				48	–1.62	32.41	6.01	70.2	0.7

TABLE I: *continued*

Date	Time	Air temp.	Ice	Depth	Temp.	Salinity	O_2	O_2	PO_4-P
day/ month		°C	cm	m	°C	‰	ml/l	% sat'n	µg-at/l
1/8	1630	5	...	0	0.40	19.94	8.33	93.4	0.2
				10	–0.79	31.42	7.98	94.3	0.3
				25	–0.86	31.87	8.02	95.0	0.3
				43	–1.41	32.30	6.33	74.3	0.6
11/8	1350	6	...	0	1.50	31.56	8.37	102.6	0.1
				10	0.42	30.21	8.78	106.3	0.1
				25	–0.42	31.20	8.80	105.0	0.1
				50	–1.11	32.09	6.90	81.5	0.2
20/8	1330	3	...	0	0.90	30.90	6.41	78.9	0.3
				10	0.79	30.90	4.51	55.3	0.3
				25	0.04	31.13	...	...	0.2
				49	–0.07	31.69	6.87	83.1	0.4
2/9	1100	1	...	0	1.80	31.04	7.22	93.3	0.2
				10	1.55	31.04	4.46	55.9	0.3
				25	1.18	31.15	4.69	58.3	0.4
				50	–0.24	31.67	4.08	49.4	0.5
13/9	1730	2	...	0	0.20	30.73	8.71	105.2	0.3
				10	0.20	30.73	8.50	102.7	0.3
				25	0.19	31.35	7.84	95.2	0.3
				50	–0.63	31.87	7.01	83.8	0.4

early May. A very slight warming (to –1.67°) was noted on the surface on May 19, but the true summer temperature climb, at 0, 10, and 25 m, was not recorded until mid-June, and at 50 m not until mid-July. The maximum temperature at the surface was 1.80°, at 10 m it was 1.55°, and at 25 m 1.18°, all on September 2; at 50 m it was –0.07°, on August 20.

SALINITY

Salinity values are shown in Fig. 2(c) and Table I. Salinity values at all depths rose from between 30.70 and 31.50‰ between late September and November to between 32.00 and 32.50 in December and January. A slight fall occurred during January, then between early February and early May values increased from between 32.00 to 32.30 to between 32.40 and 32.60. Coinciding with the first evidence of spring melting, salinity at the surface fell slowly from May 5 until June 13, then rapidly, to 27.01 on June 19, 1.68 on July 2, and lower on July 15, then rose through July and early August. Only slight summer decrease was recorded for the other depths.

The development of a brackish water layer at the surface, coinciding with ice melting, has been shown at Igloolik and elsewhere, without clear definition of the depth to which it extends. Digby (1953) recorded a low value of 5.82 at 1 m on June 5 in Scoresby Sound, a drop from 31.49 on May 25, but only a relatively slight decrease at 5 m. Ellis (1956) in Eclipse Sound, north Baffin Island,

recorded less than 8.80 from the surface, and more than 32.00 at 5 m, on June 27. More detailed measurements, made by the *Calanus* at Rowley Island in 1957 (unpublished data), showed the depth of the brackish layer to extend only to 2 m at its greatest extent. Salinity of the deeper water fell slightly during the summer, but probably not to levels low enough to inhibit plankton. As river influence was greater at the Rowley Island station than at Igloolik, it is probable that the brackish water at Igloolik was even less than 2 m thick, thus that the early summer inhibition of plant life recorded by Bursa (MS) from the surface was confined to a superficial layer only.

DISSOLVED OXYGEN

Dissolved oxygen figures, expressed as cubic centimetres per litre, are given in Fig. 2(d) and Table I. Oxygen content fell during the winter, to less than 6 cc/l in late April and May. Between May and July the content at all depths increased, to reach the summer peaks of 9.52 at the surface on July 2, 9.23 at 10 m on July 15, 8.80 at 25 m, and 6.90 at 50 m, both on August 11. In late August and early September, all values fell, to the year's low of 4.08 at 50 m on September 2. Change during the year was much smaller at 50 m than at the other depths.

Oxygen values, given as percentage saturation, are shown in Table I. Oxygen supersaturated waters occurred at the surface only on August 11 and September 2, at 10 m during all of July, and again on August 11 and September 2, and at 25 m in mid-July and again on August 11. The greatest supersaturation was found at 10 m on July 15 (110.27%). At 50 m the highest saturation value was only 83.75% on September 13. Lowest saturation values occurred in early May, at all depths, and in early September, at 10, 25 and 50 m, the lowest recorded figure being 49.39% at 50 m on September 2.

DISSOLVED INORGANIC PHOSPHATE

Figure 2(e) and Table I give data on dissolved inorganic phosphate. No determinations were made in September, October or November, 1955. Values ranged from 0.1 to 0.4 μg-at/l during December, January and early February, then fell to near zero in late February, the lowest figures of the year. They then rose at all depths, reaching 0.5 in late May. Values at the surface climbed to 1.5 in mid-June, at 10 m to 0.7 at the end of May, at 25 m to 0.7 and at 50 m to 1.1 in early July. Following these dates all values declined to 0.1 to 0.2 in mid-August, then rose slightly by early September.

THE ZOOPLANKTON

Laboratory treatment of the zooplankton was described under Methods, above. In Table II, total zooplankton volumes along with measureable volumes of the

major components are presented for each collection date, expressed as millilitres per single 50-m haul. These measurements are shown graphically in Fig. 3. The maximum quantity of total zooplankton, 4.83 ml, was collected on September 25, 1955. Volume declined in October, to 1.20 ml, then fluctuated between 0.90 and

TABLE II. Zooplankton at Igloolik, 1955–56. Quantities shown are in millilitres per 50-m haul with the No. 0xx net. Quantities less than 0.05 ml are shown by +. Unidentified material was mostly fragments of Ctenophora.

Date	Medusae	Chaetognatha	Polychaeta	Copepoda	Cirripedia	Amphipoda	Decapoda	Pteropoda	Larvacea	Unidentified	Total
25/9	1.90	0.35	0	1.25	0	0.10	0.05	0	0.10	1.10	4.85
5/10	0.30	0.05	0	0.40	0	+	0	0	+	0.45	1.20
10/11	+	0.10	0	1.05	0	0.15	0	+	+	1.10	2.40
25/11	0.05	0.10	0	0.25	0	0.90	0	0	0	0.30	1.60
8/12	+	0.05	0	0.55	0	0	0	0	+	0.30	0.90
23/12	+	0.05	0	0.35	0	+	0	0	+	0.60	1.00
10/1	0.10	0.05	0	0.40	0	0	0	0	0	1.40	1.95
25/1	0.15	0.05	0	0.25	0	0.05	0	0	+	0.60	1.10
6/2	0.35	0.05	0	0.50	0	0	0	0	+	0.65	1.55
28/2	0	0.05	+	0.10	0	+	0	0	0	0.15	0.30
13/3	+	0.05	0	0.05	0	+	0	0	0	0.15	0.25
26/3	+	0	0	0.05	0	0	0	+	0	0.35	0.40
14/4	+	+	0	0.05	0	0	0	0	0	0.10	0.15
24/4	+	+	0	+	0	0.45	+	0	0	0.15	0.60
5/5	0.05	+	+	+	0	+	0	0	0	0.45	0.50
19/5	0.05	+	+	0.10	+	+		0	0	0.10	0.25
30/5	+	0	0	+	0	+	+	0	0	0.55	0.55
13/6	+	0	0	0.05	0	+	+	0	0	0.20	0.25
19/6	+	+	0	0.05	0	0.10	0	+	0	0.60	0.75
2/7	0.30	0	0	+	0	0	+	+	0	0.35	0.65
15/7	0.05	0.05	+	0.10	+	+	+	+	0	0.10	0.30
25/7	+	0	+	0.20	+	+		+	0	0.65	0.85
1/8	+	0	+	0.20	+	+		0	+	0.20	0.40
11/8	0.20	+	+	0.20	+	+		+	+	+	0.40
20/8	0.20	0	0	0.15	0.20	+	0	0	+	0.05	0.60
2/9	0.20	+	+	0.25	0.25	0.20	0	0	+	0.40	1.40
13/9	0	+	+	0.60	+	0	0	0	+	0.20	0.80

2.40 ml between October and early February. In late February quantity fell abruptly to 0.30 ml, reached the minimal value in mid-April of 0.15 ml, then, with fluctuations, generally increased until September of 1956.

The largest single component of the plankton was unidentifiable material which consisted as far as could be determined, almost entirely of fragments of Ctenophora. Not a single ctenophore was preserved in its entirety, minute fragments of comb plates being the only recognizable remnants. Next, in volume, were the Copepoda, taken in greatest abundance (1.25 ml) on September 25. Except for a quantity of 0.10 ml taken on May 19, all volumes between March and mid-July were 0.05 ml or less. In addition, volumetric measurements were

made of Medusae, Chaetognatha, Cirripedia (larvae), Amphipoda, Decapoda and Larvacea. Volumes of Polychaeta and Pteropoda were too small for measurements.

Table III presents numbers of zooplankton individuals per single 50-m haul with No. 0xx and No. 6xxx nets. Numerically dominant, far in excess of any other taxonomic group, were the copepods. Collections of zooplankton are shown in

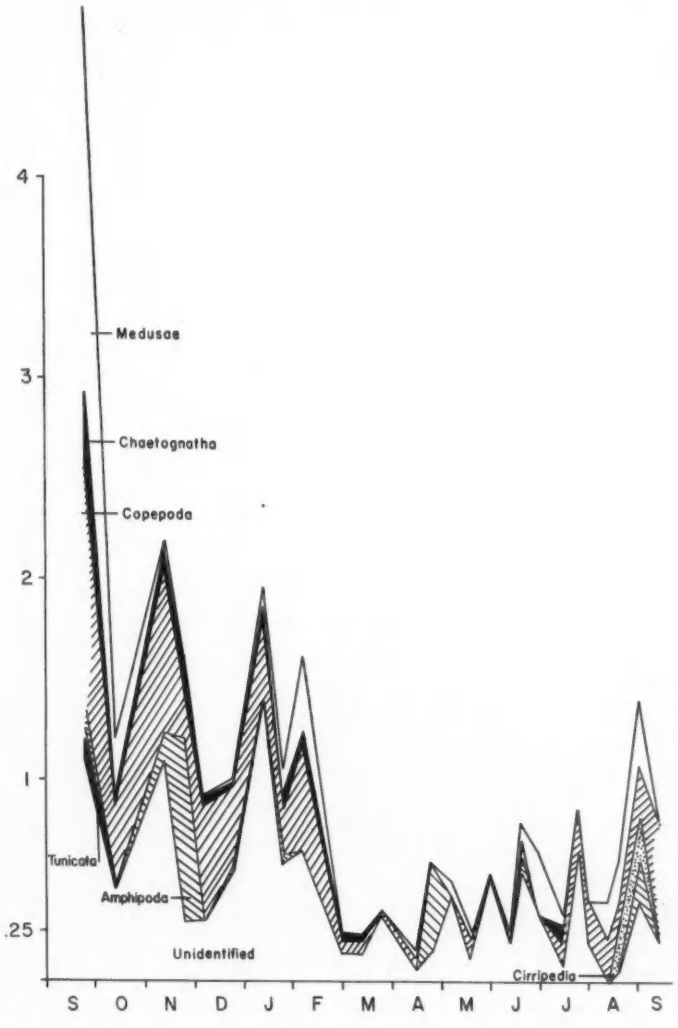

FIG. 3. Zooplankton volume, in millilitres per 50-m haul, taken with the No. 0xx net.

TABLE III. Zooplankton at Igloolik, 1955–56. Quantities shown are

	25/9	5/10	10/11	25/11	8/12	23/12	10/1	25/1	6/2	28/2	13/3
Medusae (No. 0xx)											
?Euphysa flammea	0	0	0	0	0	0	0	0	0	0	0
Halitholus cirratus	3	1	0	0	0	0	0	0	0	0	0
Tiaropsis multicirrata	0	0	0	0	0	0	0	0	0	0	0
Aglantha digitale	1	0	1	1	0	0	3	2	5	0	0
Aeginopsis laurenti	0	0	0	1	0	1	0	0	0	0	0
Cyanea capillata	0	0	0	0	0	0	0	0	0	0	1
Others	1	0	0	0	0	0	0	0	1	0	0
Chaetognatha (No. 0xx)											
Sagitta elegans	14	11	6	9	6	5	3	6	8	3	6
Polychaeta (No. 0xx)											
Autolytus alexandri	0	0	0	0	0	0	0	0	0	0	0
A. prismaticus	0	0	0	0	0	0	0	0	0	1	0
Scalibregma inflatum	0	0	0	0	0	0	0	0	0	0	0
Larvae	0	0	0	0	0	0	0	0	0	0	0
Copepoda											
Calanus finmarchicus (No. 0xx)	498	198	287	90	161	81	89	54	117	24	25
C. hyperboreus (No. 0xx)	88	9	34	8	21	13	25	19	27	5	3
Calanus spp. stage I (No. 0xx)	2	8	0	0	0	0	0	0	0	0	0
stage I (No. 6xxx)	10	17	0	0	0	0	0	0	0	0	0
Pseudocalanus minutus (No. 0xx)	1345	1217	456	491	359	268	116	102	371	333	161
(No. 6xxx)	2070	1921	1437	583	598	441	533	221	291	747	547
Metridia longa (No. 0xx)	2	0	6	1	6	5	5	8	17	4	6
Metridia longa (No. 6xxx)	0	0	0	0	5	18	9	5	0	0	0
Acartia longiremus (No. 0xx)	0	2	1	0	0	1	0	0	0	1	0
(No. 6xxx)	51	0	0	0	0	0	0	5	30	29	0
Oithona similis (No. 6xxx)	40	68	0	38	20	20	3	0	22	20	0
Oncaea borealis (No. 6xxx)	0	0	0	10	0	9	0	0	0	0	0
Harpacticus superflexus (No. 0xx)	0	0	0	0	0	0	0	0	0	0	0
(No. 6xxx)	0	0	0	0	0	0	0	0	0	0	0
Nauplii, all species (No. 6xxx)	30	0	0	0	0	0	0	0	0	0	0
Others (No. 0xx)	0	1	0	0	0	0	0	0	0	0	0
Cirripedia											
Larvae (No. 0xx)	0	0	0	0	0	0	0	0	0	0	0
Larvae (No. 6xxx)	0	0	0	0	0	0	0	0	0	0	0
Amphipoda (No. 0xx)											
Apherusa glacialis	1	0	1	1	0	0	0	0	0	0	0
Gammarus wilkitzki	0	0	1	4	0	1	0	0	0	0	0
Hyperoche medusarum	0	0	0	0	0	0	0	0	0	1	0
Themisto abyssorum	0	0	0	0	0	0	1	0	0	1	0
Decapoda (No. 0xx)											
Eupagurus sp.	0	0	0	0	0	0	0	0	0	0	0
Hippolytidae	1	0	0	0	0	0	0	0	0	0	0
Pteropoda (No. 0xx)											
Limacina helicina	0	0	1	0	0	1	0	0	0	0	0
Clione limacina	0	0	0	0	0	0	0	0	0	0	0
Larvacea (No. 0xx)											
Oikopleura vanhoeffeni	4	1	1	0	1	1	0	1	1	0	0
Fritillaria borealis	0	0	0	0	0	0	0	0	0	0	0

numbers of individuals per 50-m haul with the No. 0xx or No. 6xxx net.

26/3	14/4	24/4	5/5	19/5	30/5	13/6	19/6	2/7	15/7	25/7	1/8	11/8	20/8	2/9	13/9
3	8	0	2	1	0	1	1	0	0	0	0	0	0	0	0
0	0	4	0	5	2	3	9	7	2	2	0	1	1	1	0
0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	1	0	0	0	5	2	4	2	7	5	3	3	3
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	7	0	1	0	0	11	26	127	104	40	2	2
4	4	3	3	8	1	24	19	10	40	36	18	35	197	267	610
0	2	2	1	1	0	3	3	2	9	10	38	39	43	13	33
0	0	0	0	0	0	0	1	1	5	3	23	57	151	37	21
0	0	0	0	–	0	0	–	5	0	3	80	175	250	200	130
56	134	75	29	457	22	159	148	48	225	215	368	155	282	230	1001
236	815	498	178	–	382	241	–	47	170	228	1421	1309	1879	2369	1818
1	0	0	0	0	0	1	0	0	1	2	0	1	0	0	0
0	0	0	0	–	0	0	–	3	0	0	0	0	0	0	0
0	2	2	0	0	0	1	0	0	0	2	0	2	0	1	0
0	0	0	0	0	0	0	–	0	0	0	15	0	0	24	42
0	35	6	0	–	4	61	–	3	3	0	10	49	61	0	10
0	0	0	0	–	0	10	–	0	0	4	0	0	0	0	12
0	0	0	0	0	0	0	1	1	9	2	1	0	0	0	0
0	0	0	0	–	0	0	–	3	5	3	10	0	0	10	0
0	0	5	50	–	60	330	–	23	85	360	1370	525	780	280	220
5	10	0	0	0	0	11	0	4	0	2	1	0	0	0	19
0	0	0	0	4	0	0	0	0	22	70	c.200	c.300	c.900	c.900	35
0	0	0	+	+	+	+	+	+	+	+	+	+	+	+	+
0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
0	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	3	0	1	1	1	1	1	0	0	0
0	0	0	0	0	0	0	1	1	8	2	0	2	1	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	3
0	0	0	0	0	0	0	0	0	0	0	11	182	216	3	34

graphs in Fig. 4, given as primarily carnivorous and herbivorous zooplankton separately (this distinction is discussed below). As the herbivorous zooplankton represented the great bulk of individuals taken, it is the curves for this group

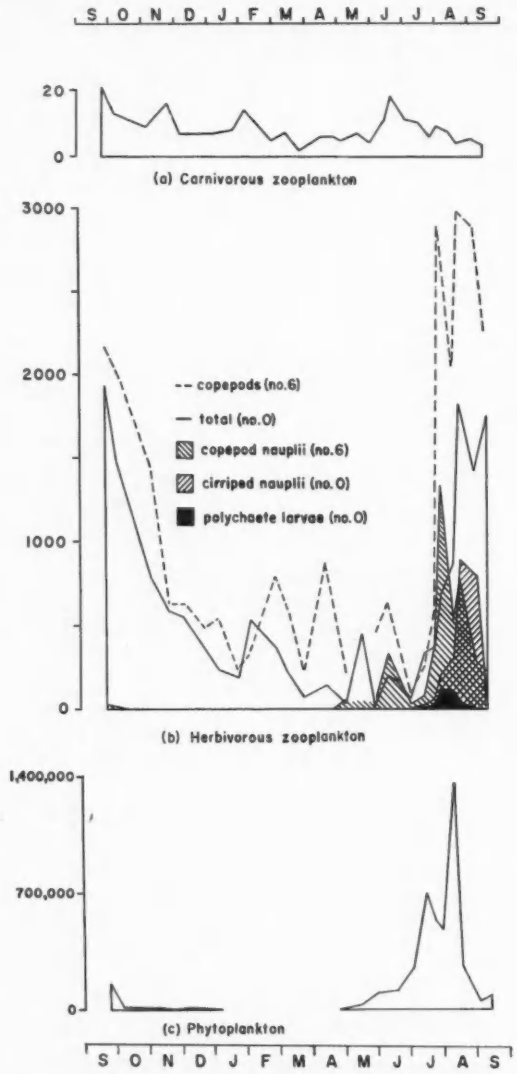

FIG. 4. Zooplankton individuals, expressed as number of specimens per 50-m haul of (a) predominantly carnivorous zooplankton, and (b) predominantly herbivorous zooplankton. (c) phytoplankton individuals, as number of cells per litre averaged for the four sampled depths.

which approximate the annual numerical cycle in the zooplankton, best illustrated by the upper, broken-line curve in Fig. 4(b) of copepods taken with the No. 6xxx net. Here, numbers declined rapidly during September to November, then slowly until January. Three small peaks occurred in February, April and June, before the season's minimum in early July. Following this time, numbers increased sharply, maximum populations occurred in August, and numbers declined in September. (The later peak in the No. 0xx net hauls, shown in the same figure, was caused by sampling favouring larger individuals which had become more numerous at the end of the summer growing season, discussed below.)

Reference was made, above, to the influence upon the plankton collections of the water movements of northwestern Foxe Basin, and to the southeasterly flow through Fury and Hecla Strait. A result of this was that a more or less constantly changing plankton population was probably in passage through the collection area during the entire year. Examination of Fig. 4(b) helps to illustrate this. Assuming a real increase in the February collections, the most probable explanation is invasion of the collecting region by animals from outside the area. It is suggested, from this, that part of the early winter decline may have been caused not only by mortality, but also by movement away from the collecting area, replacement by a still-surviving population having taken place in February. Another decline followed February, and further fluctuations occurred until early summer. Starting at least as early as May, there were additions to the plankton of animals (copepods) not newly produced but obviously winter survivors, which had not been taken by the net hauls during the winter. Further additions appear to have occurred during the summer period, especially of copepods, probably produced outside the collection station and subsequently introduced. It is difficult to explain these movements at Igloolik. Similar variations in the plankton in other areas have been attributed to vertical migrations, but vertical movements were of unlikely occurrence at the Igloolik station, sampling having been done from the bottom to the surface. Such movements, therefore, must have been at least partly horizontal, possibly associated with vertical migrations in adjacent deeper waters. It is possible that the waters to the north and northwest, deeper than Igloolik, supported a population of zooplankton only occasionally represented in the Igloolik collections. It is suggested that the total quantity of zooplankton in the water masses adjacent to Igloolik did not fall to the very low level of the Igloolik collections, but that part of the over-wintering zooplankton may have resided in deeper water, appearing from time to time in the upper water layers either by the agency of varying water movements or by active vertical migration of the animals. The spring rise and a possible subsequent summer rise may be related in time with phytoplankton food availability in the upper layers, the autumn descent with phytoplankton depletion. This, however, will not explain mid-winter rise for which light has been suggested as a possible factor elsewhere (Digby, 1954).

In the accounts of species, below, reference is made to general distribution and more specifically to North American localities adjacent to Foxe Basin from which distributional records exist. The terms "arctic" and "subarctic" are used as in previous publications of this series, as defined by Dunbar (1951).

Medusae

Medusae (Table III) occurred on 25 of the 27 collection dates, and were one of the few groups present during the entire year. In quantity of biomass, they were most abundant in late September 1955 (Table II; Fig. 3), with lesser peaks in February, July, August and early September, 1956. The February peak consisted entirely of one species (*Aglantha digitale*), that of July to September almost entirely of another (*Halitholus cirratus*). The large late September biomass consisted of few but large individuals.

Anthomedusae

Euphysa flammea (Linko)

This is a subarctic, arctic species, probably circumpolar, recorded from the eastern North American coast only from Exeter Sound, east Baffin Island (Kramp, 1942a) and to the west from northern Alaska (Bigelow, 1920; MacGinitie, 1955).

The only Igloolik specimen which can be placed with reasonable certainty in this species is a 6-mm high individual taken on May 19. Several smaller specimens, collected between March 26 and June 19, from about 1.5 to 3 mm bell height, are probably young representatives of the same species. If this is correct the production of young begins before the end of March, thus occurs during winter.

Halitholus cirratus Hartlaub

This is an arctic, subarctic, circumpolar species, known along the eastern American coast from Jones Sound (Kramp, 1942a) south to Newfoundland (Frost, 1937), and to the west from Alaska (Bigelow, 1920).

At Igloolik, it was taken in September and October 1955, and from April to September 1956, and was absent from the collections from October until April. The largest collection

Table IV. Specimens of *Halitholus cirratus* captured at Igloolik, 1955–56.

Date	Number	Mean bell height	Approximate mean tentacle number
		mm	*no.*
25/9	3	16	35
5/10	1	15	–
24/4	8	1	9
19/5	14	2	12
30/5	5	1	13
13/6	10	1	15
19/6	26	2	16
2/7	22	3	19
15/7	6	3	19
25/7	6	5	23
11/8	2	7	24
20/8	1	9	29
2/9	1	9	32

(9 specimens per haul) was taken in June. The largest individuals, 15 to 16 mm bell height, were found in September and October, and had well developed gonads. Three of these, averaging 16 mm in height, had a mean number of about 35 tentacles. The next collection, taken in April, consisted of 8 specimens, averaging about 1 mm in height and showing a mean tentacle number of about 9. Increase in bell height and tentacle number, especially from June until early September, is shown in Table IV. Gonads were large in late September and October medusae. There is evidence of late winter and spring release of young, which

during April, May and June, at least, were as small as 1 mm. Principal growth of the young medusae evidently occurred during spring and summer, reaching maximum size by September, between which time and late winter and spring the next generation apparently reached the medusa stage. There is probably a single generation per year, with the life span completed within a single year.

LEPTOMEDUSAE

Tiaropsis multicirrata (M. Sars)

This species is recorded only from Clyde River (eastern Baffin Island) in the eastern Canadian arctic (Dunbar, 1942b). It is known from West Greenland south along the eastern American coast to Woods Hole, northeast of the Atlantic to the Barents Sea, and in the North Pacific and north of Bering Strait (Kramp, 1942a). From these records it appears to be largely a subarctic and boreal species, and for this reason its occurrence at Igloolik (and in other parts of Foxe Basin, unpublished records) is interesting.

Only one specimen occurred, an individual 8 mm in diameter, taken on August 1.

TRACHYMEDUSAE

Aglantha digitale (O. F. Müller)

This is an arctic, subarctic, circumpolar species, known from as far north as Smith Sound (Kramp, 1942a) and to the west from Dolphin and Union Strait (Bigelow, 1920) and Fort Ross (Somerset Island) (Dunbar, 1942a).

At Igloolik, *Aglantha digitale* was taken in increasing numbers from late September 1955, to early February 1956, and during the rest of the year only once, in mid-July. The largest individual was only 18 mm in height, with gonads up to 1.5 mm long. Heights and maximum gonad lengths are shown in Table V. While there is little evidence of size increase during the September to February period, maximum gonad length shows a fairly regular increase. The total absence of large individuals and the apparent disappearance of all members of the

TABLE V. Specimens of *Aglantha digitale* captured at Igloolik, 1955–56.

Date	Number	Bell height range	Maximum gonad length
		mm	*mm*
25/9	1	8	0.3
10/11	2	6–8	0.4
25/11	1	6	–
10/1	10	5–12	0.6
25/1	7	6–8	0.6
6/2	15	6–18	1.5
15/7	2	8–9	1.0

species after early February implies distribution at a greater depth than the Igloolik station. Kramp (1942a), referring to *A. digitale* of waters west of Greenland, found it most abundant at 50 m, and numerous from 50 to 200 m. He also reported the species present in the plankton all year, and young medusae present at all times, from which he concluded that propagation occurred at all seasons. In Danish waters, Kramp (1927) found a one-year cycle, with most young produced in the spring and early summer. Linko (Kramp, 1947) concluded propagation takes place chiefly in winter in the Barents Sea. Kramp (1947) found most large specimens in deep (less than 0°C) water, most young in the upper, warmer water layers, a situation similar to that noted by Østvedt (1955) in the Norwegian Sea, where

full-grown individuals were always taken below 100 m, and in June and July many small specimens were found in the upper 100 m, mostly in the 50-to-0-m layer. Østvedt concluded that spawning occurred in late spring or early summer.

Table VI shows bell heights and maximum gonad lengths for 15 individuals taken on February 2, 1956. Here gonads are readily discernible in medusae of 6 and 7 mm in height, but in the largest specimen, 17 mm high, the gonads are only 1.5 mm long. Kramp (1942a) has pointed to the appearance of gonads in smaller medusae in coastal waters than in the open sea, giving minimum heights of 5 to 7 mm for West Greenland coastal waters and 10 to 11 mm for farther offshore waters. He has given also representative gonad lengths for

TABLE VI. Relation of bell height to maximum gonad length in *Aglantha digitale* at Igloolik, 1955–56.

Bell height	Maximum gonad length	Bell height	Maximum gonad length
mm	*mm*	*mm*	*mm*
18	–	8	0.6
17	1.5	7	0.9
10	1.3	7	0.8
10	1.3	7	0.7
9	1.3	7	0.7
9	0.7	7	0.5
8	0.7	6	0.4
8	0.6		

larger individuals, showing gonads of 5 to 7 mm in length for medusae 17 mm in height. From these examples, the Igloolik medusae appear to develop discernible gonads at as small a size as the inshore West Greenland specimens, but the larger individuals show much smaller gonads than medusae of similar size from waters west of Greenland. This may denote slower gonad development, after their initial appearance, in the Igloolik medusae, or it may simply be indicative of winter retardation of gonad growth, the larger Igloolik specimens having been sampled in winter, the West Greenland medusae in summer.

Absence of full-grown individuals from the Igloolik collections suggests that, as reported from elsewhere, the larger medusae seek deeper water than the 50-m depth of the collecting station, that young may appear in deeper water and rise, while still of small size, to the upper water layers. The existence of small medusae of similar size from July until at least February implies a long period of propagation, occurring, at least partly, during the winter.

NARCOMEDUSAE

Aeginopsis laurenti Brandt

An arctic, subarctic species, it is probably circumpolar, recorded in eastern North America from Smith Sound to Newfoundland (Kramp, 1942a), from Lake Harbour (Hudson Strait), and to the west from Fort Ross (Somerset Island) (Dunbar, 1942a), and from northern Alaska (Bigelow, 1920).

Two individuals only were found at Igloolik, one of 10 mm diameter on November 25 and one of 7 mm diameter on December 23. According to Kramp (1942a, p. 100) it is a distinctly cold water species; it exhibits no definite breeding period, but "propagates when and where the water is cold".

SCYPHOMEDUSAE

Cyanea capillata (L.)

This species is arctic, subarctic, boreal and circumpolar. Its eastern American records include Jones Sound (Kramp, 1942a) and the Strait of Bell Isle (Whiteaves, 1901, as *C. arctica*). Westward, it is known from Alaska (Bigelow, 1920).

Only 9 individuals were taken at Igloolik, between March and July, as shown in Table VII. From 3.5 mm in diameter on March 13, individuals reached 26 mm on July 2. This suggests liberation of young at least as early as March, and from the presence of a 12-mm specimen in mid-July, to propagation extending at least into spring. Kramp (1942a) referred to rapid growth in the waters west of Greenland. He inferred liberation of young medusae from May to July. By September many were large adult forms. No adults were collected at Igloolik.

TABLE VII. Number and size of specimens of *Cyanea capillata* taken at Igloolik, 1955–56.

Date	Number	Diameter (*mm*)
13/3	4	3.5; 5; 5; 6
5/5	2	8; 11
13/6	1	16
2/7	1	26
15/7	1	12

Chaetognatha

Chaetognaths, represented by only one species, were taken on all but five collection dates. In terms of biomass, they were most plentiful in late September 1955 (0.35 ml per haul), and least abundant from March to June, and during August and early September 1956 (Table II and Fig. 3). Individuals were most numerous in November and February, least numerous from March to June (Table III). As with the medusa *H. cirratus*, the great biomass of late September 1955 represented a comparatively small number of larger than average individuals.

Sagitta elegans Verrill

Chiefly arctic, also subarctic, and probably circumpolar, specimens referred to the form *arctica* are reported from as far north as Smith Sound (Kramp, 1939), and to the west from Alaska (MacGinitie, 1955) and Fort Ross (Somerset Island) (Dunbar, 1942a).

The 231 specimens of *Sagitta* collected range in length from 4 to 42 mm, and include no mature individuals. The total absence of mature specimens may be a result of their having escaped the nets or to their absence from the collection area. In West Greenland, Kramp (1939) found mature forms most often in considerably deeper water than the 50 m sampled at Igloolik. He suggested propagation in deep waters, rising of eggs, and hatching and development of the young in the upper water layers. Østvedt (1955) found, in the Norwegian Sea, that most specimens taken above 100 m were less than 10 mm long, occurred chiefly in June and July, and probably originated in late spring and early summer.

Estimates of times of propagation vary in different regions; April or May to August or September, West Greenland (Kramp, 1939); February to May or June, East Greenland (Ussing, 1938); June or July to October, Baffin Island (Dunbar, 1941). The occurrence of 4- and 5-mm long individuals in early August suggests that some of the Igloolik population at least were produced during the summer. The duration of the propagation period cannot

be given, although the finding in December of specimens only 5 mm long suggests breeding as late as fall or early winter.

A more detailed account of the Igloolik *Sagitta*, along with those from other localities in the eastern Canadian arctic, will appear as a subsequent number of the *Calanus* series.

Polychaeta

Pelagic polychaetes are of comparatively infrequent occurrence in cold northern waters. As such forms too are often agile enough to evade a slowly moving net, the yield in the Igloolik collections was small.

Syllidae

Autolytus alexandri Malmgren

This is principally an arctic, subarctic species, recorded from West Greenland (Wesenberg-Lund, 1950), Frobisher and Ungava Bays (Grainger, 1954), and to the west from northern Alaska (Pettibone, 1954).

One specimen only was taken, on July 25, a *Sacconereis* form, 9.2 mm long, with 14 anterior and 26 median segments. It carried no eggs.

Autolytus prismaticus (Fab.)

This is an arctic, subarctic species, recorded from as far north as Ellesmere Island (McIntosh, 1879), south to Labrador (Moore, 1909), to the west from Dolphin and Union Strait (Chamberlain, 1920), and possibly from Foxe Basin (Treadwell, 1937, as *Polybostrichus longosetosus*). Pettibone's (1954) revival of *A. fallax* Malmgren confuses former records of this species.

Only two specimens were taken. One, a *Polybostrichus* stage, 6 mm long, with 6 anterior and 25 median segments, was found on February 28. The second, a *Sacconereis* form, about the same length as the male, carried ventrally a large number of eggs of about 0.9 mm in diameter. This was collected on May 30.

Scalibregmidae

Scalibregma inflatum Rathke

This is a cosmopolitan species, recorded from as far north as Thule, Greenland (Wesenberg-Lund, 1950), and from northern Alaska (MacGinitie, 1955).

One specimen only was collected, on May 5, a pelagic form 7 mm long, with setae up to 0.7 mm in length.

Larvae of Polychaeta

Young pelagic larvae, including at least members of the families Spionidae and Polynoidae, were taken on all collection dates between May 19 and September 13, and at no other times during the year.

Copepoda

The copepods, in numbers of individuals, represented by far the largest single zooplankton group in these collections. Variations during the year in volume and number are given in Tables II and III, and in Fig. 4. Eight species were identified. Most abundant in the collections was *Pseudocalanus minutus*; others found in large numbers throughout the year were *Calanus finmarchicus, C. hyperboreus* and *Oithona similis*. Smaller numbers of *Metridia longa, Acartia longiremus, Oncaea borealis* and *Harpacticus superflexus* were included.

TABLE VIII. Copepod nauplii, of all species. Number of specimens per 50-m haul in No. 6xxx net, and occurrence (+) in No. 20 net, at Igloolik, 1955–56.

Date	Number 6xxx	20	Date	Number 6xxx	20
25/9	30	+	24/4	5	+
5/10	0	+	5/5	50	+
10/11	0	+	19/5	–	+
25/11	0	+	30/5	60	+
8/12	0	+	13/6	330	+
23/12	0	+	2/7	23	+
10/1	0	0	15/7	85	+
25/1	0	0	25/7	360	+
6/2	0	0	1/8	1370	+
28/2	0	+	11/8	525	+
13/3	0	+	20/8	780	+
26/3	0	+	2/9	111	+
14/4	0	+	13/9	220	+

NAUPLII

Nauplii of the copepods were not identified to species. Table VIII gives data on copepod nauplii taken with No. 6xxx and No. 20 nets, and Fig. 5 shows nauplii occurrence. The No. 20 net hauls, as explained above, could not be used quantitatively; they do indicate, however, the presence of a few nauplii in the plankton during almost the entire year, January 10 and 25 and February 6 being the only dates when none was recorded. At least two distinct peaks in nauplii occurrence are apparent in Fig. 6, a small one in mid-June, and a larger one in early August.

CALANIDAE

Calanus finmarchicus (Gunnerus)

Of this widely spread species there are many records from northern North America, from as far north as Smith Sound (Jespersen, 1934), to the west from Alaska (Willey, 1920), and from Hudson Bay (Willey, 1931). Recent investigations (Yashnov, 1955) cast some doubt on the identity of many specimens referred to this species.

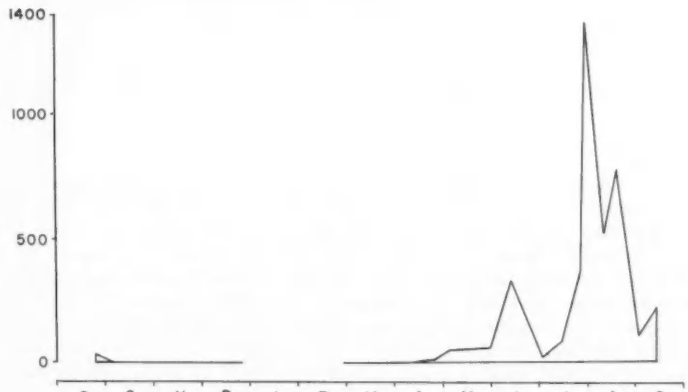

FIG. 5. Frequency occurrence of copepod nauplii, in number of individuals per 50-m haul, taken with the No. 6xxx net. The single base line shows occurrence in the No. 20 net.

Occurrence during the year of stages II to VI of *C. finmarchicus* is given in Table IX, and is shown by a series of curves in Fig. 6. In stage I, *C. finmarchicus* and *C. hyperboreus* were not separated; Table IX and Fig. 6, therefore include stage I representatives of both species combined. Because of the difficulty in distinguishing between the two species in both nauplii and stage I, the precise time of appearance of these stages in the plankton cannot be given. It probably occurred, however, during July, with the maximum occurrence of nauplii at the end of July and of stage I around mid-August. The last evidence of *Calanus* nauplii was in September, and of stage I (probably all *C. finmarchicus* this late in the season) in October. Stage II appeared in small numbers about mid-July, then increased rapidly to maximum numbers in late August, disappearing from the plankton in October, and reappearing, as only

TABLE IX. *Calanus finmarchicus*. Numbers of specimens per 50-m haul (No. 0xx net for stages II–VI; No. 0xx and No. 6xxx nets for stage I, identified as *Calanus* sp. only), taken at Igloolik, 1955–56.

Date	*Calanus* sp. St. I 6xxx	*Calanus* sp. St. I 0xx	St. II	St. III	St. IV	St. V	Stage VI ♀	Stage VI ♂	Total
25/9	10	2	53	99	182	159	4	1	498
5/10	17	8	58	67	52	20	1	0	198
10/11	0	0	0	53	137	89	4	4	287
25/11	0	0	0	32	34	23	1	0	90
8/12	0	0	0	33	67	53	3	5	161
23/12	0	0	1	22	35	17	3	3	81
10/1	0	0	0	12	45	20	7	5	89
25/1	0	0	0	13	21	6	6	8	54
6/2	0	0	0	21	48	23	16	8	117
28/2	0	0	0	12	6	3	2	1	24
13/3	0	0	0	10	9	2	3	1	25
26/3	0	0	0	1	2	1	0	0	4
14/4	0	0	0	3	1	0	0	0	4
24/4	0	0	0	2	0	0	1	0	3
5/5	0	0	0	1	1	1	0	0	3
19/5	0	0	0	7	1	0	0	0	8
30/5	0	0	0	1	0	0	0	0	1
13/6	0	0	0	15	9	0	0	0	24
19/6	0	1	0	14	5	0	0	0	19
2/7	5	1	0	2	7	1	0	0	10
15/7	0	5	1	13	19	6	1	0	40
25/7	3	3	1	1	20	11	3	0	36
1/8	80	23	0	1	10	6	1	0	18
11/8	175	57	13	5	7	10	0	0	35
20/8	250	151	150	41	4	2	0	0	197
2/9	200	37	159	102	4	2	0	0	267
13/9	130	21	105	377	112	16	0	0	610

one individual, in late December. The absence of nauplii, stage I and stage II from the collections, respectively from September until July, from October until July, and from December until July, suggests either extinction of these stages during this period or survival at depths untouched by sampling. In both nauplii and stage I there is no evidence for survival, but in stage II, the single December specimen and the two in July, preceding the sharp August increase of the new generation, suggest the possibility of winter survival. With stage III, it is apparent that members of the group did survive throughout the year. There was a rapid increase from about mid-August until early September, then a gradual decline through the fall and winter to minimum numbers in April and May. Of special interest here was the number of specimens taken during June and July, and the decline in late July and early August, preceding the rapid increase of about mid-August, referred to above. In the assumption that the early September peak of stage III represents development from nauplii through stages I and II of individuals in their first summer and that the mid-August numerical growth

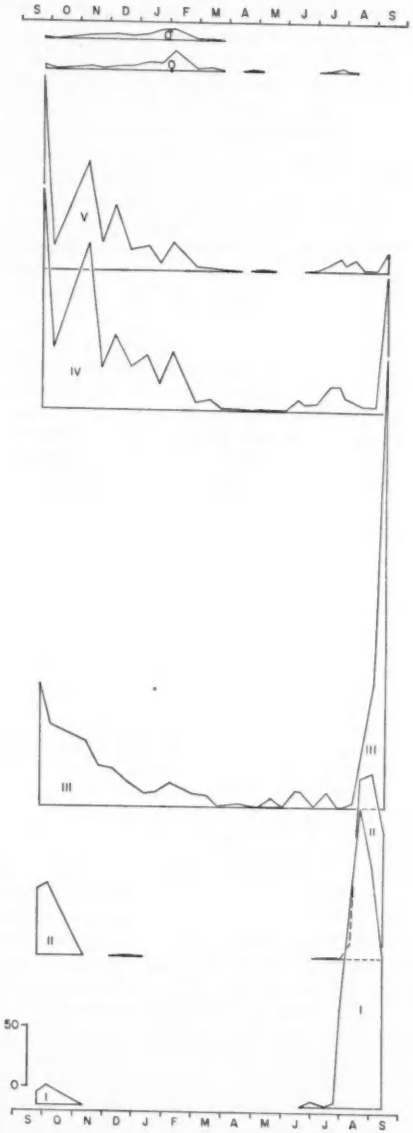

FIG. 6. Frequency of occurrence of *Calanus finmarchicus*, in number of individuals per 50-m haul, taken with the No. 0xx net. Stage I is of *Calanus* spp. combined.

in stage III followed from the early August increase of stage II, the appearance of stage III specimens in May, June and July must represent copepodites of at least the previous summer's brood. The relatively large number of these in the plankton, compared with the low population apparently present from March to May, can best be explained by vertical migration, these individuals having dropped to greater depths than 50 m, perhaps in March, and having risen to the upper waters in May and June.

In stage IV, there was a definite increase in population during September, with the peak probably occurring in late September. An abrupt decrease in October, and an equally definite increase in early November, were followed by a gradual falling off of the population until April and early May. There was then a growth in population until July, followed by a drop preceding the early September rise. A situation similar to that found in stage III is suggested, with young of the year reaching maximum numbers in late September, falling off during the

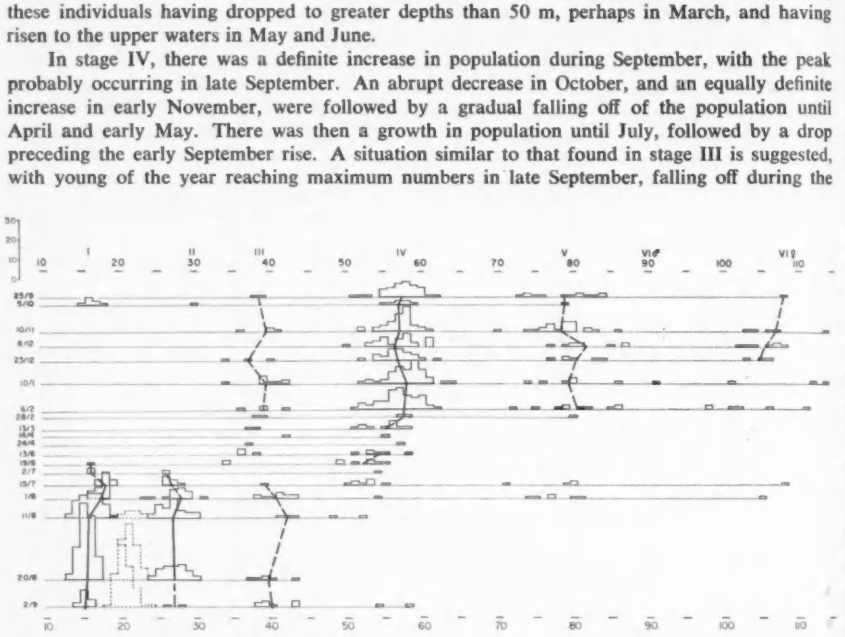

FIG. 7. Cephalothoracic length frequency histograms of stages II to VI of *C. finmarchicus*. Stage I is of *Calanus* spp. combined. The dotted lines show stage II of *C. hyperboreus*, separated from *C. finmarchicus* on size only. The heavy lines join mean lengths of adjacent histograms. Lengths are in micrometer units (1 unit = 0.063 mm).

winter, possibly moving into deeper water in March and returning in the upper layers in May. The increase in June may have represented individuals still in stage IV from the previous autumn; increased numbers through to August, however, may represent additions to the stage of individuals newly developed from stage III. The occurrence of stage V individuals followed closely that of stage IV. There was evidence of a less steep rise in numbers in early September thus the peak probably was reached slightly later in September than in stage IV. Evidence for vertical migration is not so great in this stage as in the two preceding. Decline in numbers in late February may have been due to development to stage VI and to natural mortality rather than to migration to deeper water, as the population in July and August, preceding the September rise of presumably young specimens of the year, may have been developed in the upper layers from recently risen stages III and IV. Both males and females of stage VI occurred most plentifully in January and February, females from September to April, and again in July, and males from September to March. Members of stage VI probably developed partly from stage V of the year during early winter, partly from older stage V during the summer. Most of the life cycle of adult specimens may have been spent in deeper water, rising to the upper layers chiefly during January and February.

Figure 7 shows cephalothoracic length frequencies of specimens of stages of *C. finmarchicus*, lengths expressed in micrometer units (1 unit = 0.063 mm). The heavy lines join mean

length values of adjacent histograms. While many of the samples are too small to be of value, something can be learned of size change in stages III, IV, and V between September and February, and in stages I (*C. finmarchicus* and *C. hyperboreus* combined, but chiefly of *C. finmarchicus*), II, III and IV between June and September. The figure shows a decrease in the mean length of stages III, IV and V between September and December, most obvious in stage III where the addition to the stage of progressively smaller individuals and the loss of larger individuals is clearly demonstrated. In stage III there was a marked rise in the mean length in early January, then decreasing length into the winter. A similar change is suggested in stage IV, but does not appear in stage V. In stages I and II there was a slight decrease in length from July and August until September. In stage III there was a decrease in length between May and June, an increase until August, then a falling off of the mean length until September. Stage IV shows length increase from June until August. The picture in stage VI is less clear, although there is a suggestion of maximum length in both males and females having been reached in December, with subsequent reduction in mean length until at least February.

Such size changes as these may be used to give some hint of the history of individuals of the various stages. It has been suggested by several workers that temperature at the time of moult acts as a controlling factor in determining the size of the individual after moulting. Ussing (1938) proposed that the size reached by a copepod following moulting was dependent upon two main factors: the size of the individual preceding the moult, and the nutritional conditions prevailing at the time of moulting. Digby (1954) suggested that the size before moulting had no effect upon subsequent size, which was dependent entirely upon conditions at the time of the moult.

In Fig. 7 the largest mean lengths of stages I, II, III and IV are found close to the time of the first appearance of first-year members of these stages in the plankton. These represent copepodites produced from nauplii and developed to at least stage IV during the period from July until soon after mid-August, at a time of abundant phytoplankton (Fig. 4). Succeeding collections of these stages show gradually diminishing mean length until mid-September 1956, and from late September 1955 until early winter. It is probable that most of these specimens were produced from nauplii of the preceding summer, and that the farther into the summer and fall development occurred, after the phytoplankton maximum, the smaller the copepodite stages developed from them became. In late August phytoplankton diminished greatly, and during September, October and November continued depletion of phytoplankton meant gradually falling food supplies. Thus copepodite length decrease accompanied diminishing food supply, and individuals moulting from one stage to the next became progressively smaller than members inhabiting the same stage immediately before them. Accompanying this size reduction and slowing growth rate was a probable slowing down of the rate of moulting. While the earliest individuals appear to have developed from nauplii to at least stage V within a period of less than 6 weeks, later nauplii probably were transformed more slowly into copepodites which in turn underwent less rapid moulting than the earliest individuals.

Maximum size of the copepods was reached before sea temperatures rose to their summer peak, highest temperatures, in September, occurring while copepods were diminishing in size. Better correlation appears to exist with phytoplankton occurrence, copepod size increasing during times of phytoplankton abundance, decreasing during times of phytoplankton scarcity. All stages, however, did not achieve maximum size at the same time, and indications are that the descendants of the earlier nauplii, produced at a time when phytoplankton supply per individual nauplius was at its greatest, reached the greatest length during the summer. The size before moulting, therefore, may have had some effect upon the size of the succeeding stage, but it is probable that conditions of feeding at the time of moulting acted as the strongest factor in determining post-moulting size.

Most noticeable in stage III and less evident in stage IV was a length increase on January 10, showing a loss of smaller and a gain of larger individuals than those found in the December 23 sample. Such a change is difficult to account for except as a result of additions to the populations at the collecting station (an explanation supported by similar

changes in other plankton species, below). Mean length values as low as those of late December were not found again until the end of February, in stages III and IV. Such an invasion of *Calanus* may have resulted from movements from greater depths than 50 m from outside the collecting area, and subsequent drifting to the Igloolik location, and consisted of larger individuals than those which occupied the station immediately before. Such changes are not readily apparent in stages V and VI.

Stage III declined in late March and April, reappeared as large individuals in May, declined again in late May, and reappeared a second time as small individuals in mid-June. The May samples may have represented another influx of copepodites from deeper waters, the June sample a further addition of specimens, in length like those of March, to the upper layers. Between June and August, when the first of the year's young reached stage III, mean length increased. This means that successively larger individuals entered the collections which they may have done through larger specimens which survived the winter reaching the surface layers, or through development from stage II copepodites, the mean length of moulting specimens thus increasing during this period of abundant food supply. The history of stage II between October and August is uncertain. Present still in large numbers in early October, it disappeared from the collections in November, reappeared as one individual in December and again as only two individuals in July, before the abrupt burst of stage II of the new generation in August. There is a possibility that its rapid disappearance in November may have been a movement to deeper water, and that the three scattered collections following may have been of strays from the centre of population out of reach of the collecting nets. This interpretation is supported by the apparently continuing development of new members of stage III through November and December, at a time when stage II was conspicuously absent from the collections. If correct, this could explain increasing length development in stage III between June and August, from a continuing reservoir of stage II. It would mean too that stage II and not stage III was the first of the winter-surviving stages. The size increase in stages IV and V between June and July probably reflects development from stages III and IV during this food-rich period.

From the information above, the life cycle appears to occur as follows: first nauplii, July; first stage I, late July, first stage II, early August, first stage III, mid-August; first stage IV, late August; first stage V, early September; first stage VI, probably autumn or early winter. While nauplii have probably disappeared by early October, and stage I by November, there is evidence that some stage II individuals may have survived through the winter, until at least June. It is clear that some specimens of stages III, IV and V did remain in the plankton all winter, and that part of the reduction in numbers in winter was due to movements out of the collecting area, probably to sinking to below 50 m, in March, and rising again to the upper waters in June and perhaps July. Rising numbers of stage III, in June, appear to have developed recently from unseen stage II, probably at depths below 50 m. Subsequent development from these through stages IV and V and probably to stage VI occurred between June and late July. Thus two parallel lines of development, one consisting of young in their first summer, the other of animals at least one year old occurred. Final achievement of the adult stages appears to have been reached, in part of the population at least, probably those which began development earliest in the summer, within a single year. Others, probably beginning the cycle later in the season, were delayed, perhaps as early as stage II, or in stages III, IV, or V, and following a winter in one of these stages, resumed growth in the following spring and were at least one year old on reaching stage VI. It is conceivable that some may have spent more than one winter in intermediate stages, and were therefore at least 2 years old on achieving stage VI. There is evidently only one brood produced per year, thus the majority of mature adults were either of the order of 7 to 8 months (from the first nauplius stage) or 19 to 20 months old at the time of breeding.

This life-history interpretation agrees in its essentials with Digby's (1954) conclusions from Scoresby Sound, East Greenland. While in Scoresby Sound development occurred to stage I in June and to stage III in July, comparable stages were not reached at Igloolik until late July and mid-August. In Scoresby Sound the reappearance of nearly one-year old

members of stage III in the upper layers occurred in April, with subsequent development to stage VI through May and June, while at Igloolik these events took place in May and through June and July. In the occurrence of such phases of the cycle, the East Greenland appears to precede the Igloolik cycle by about one to one and one half months. The only North American subarctic area from which the life history of *C. finmarchicus* has been studied, based upon summer collections only, is Ungava Bay (Fontaine, 1955). Breeding was suggested as ending in late June or early July, and the most abundant copepodite stages present during the entire summer were I, II, and III. Development of adults from these was suggested as possibly not occurring until the following year, to breed in the following spring. The possibility of a small part of the population engaging in a second breeding period in late summer or fall was suggested.

Calanus hyperboreus Krøyer

This species is widely distributed in far northern seas and in the North Atlantic and North Pacific. Its northern American distribution records are similar to those of *C. finmarchicus*, except that it is not recorded from Hudson Bay.

TABLE X. *Calanus hyperboreus*. Numbers of specimens per 50-m haul taken at Igloolik (No. 0xx net for stages II–VI; No. 0xx and No. 6xxx nets for stage I, identified as *Calanus* sp. only).

Date	*Calanus* sp. St. I 6xxx	*Calanus* sp. St. I 0xx	St. II	St. III	St. IV	St. V	Stage VI ♀	Stage VI ♂	Total
25/9	10	2	0	2	73	13	0	0	88
5/10	17	8	1	0	7	1	0	0	9
10/11	0	0	0	1	23	8	2	0	34
25/11	0	0	0	1	3	4	0	0	8
8/12	0	0	0	0	14	4	3	0	21
23/12	0	0	0	1	9	2	1	0	13
10/1	0	0	0	3	18	2	1	1	25
25/1	0	0	0	1	8	8	2	0	19
6/2	0	0	0	1	20	3	2	1	27
28/2	0	0	0	1	1	1	0	0	3
13/3	0	0	0	1	4	0	0	0	5
26/3	0	0	0	0	0	0	0	0	0
14/4	0	0	0	1	1	0	0	0	2
24/4	0	0	0	1	1	0	0	0	2
5/5	0	0	0	1	0	0	0	0	1
19/5	0	0	0	0	1	0	0	0	1
30/5	0	0	0	0	0	0	0	0	0
13/6	0	0	0	1	2	0	0	0	3
19/6	0	1	0	1	2	0	0	0	3
2/7	5	1	1	0	1	0	0	0	2
15/7	0	5	3	1	3	1	1	0	9
25/7	3	3	3	1	3	2	1	0	10
1/8	80	23	19	11	1	6	1	0	38
11/8	175	57	34	3	2	0	0	0	39
20/8	250	151	37	6	0	0	0	0	43
2/9	200	37	2	9	2	0	0	0	13
13/9	130	21	0	15	18	0	0	0	33

The annual cycle appears to be essentially similar to that interpreted for *C. finmarchicus*, although shifted ahead in time of first summer appearance by possibly as long as 4 weeks. The frequency of stages taken during the year is given in Table X, and is shown in Fig. 8, length frequency histograms of the different stages in Fig. 9.

The first nauplii of *C. hyperboreus* probably appeared in late May, the first of stage I in June (as in Fig. 6, stage I of *C. hyperboreus* and *C. finmarchicus* are combined). Stage II appeared in late June, stage III at the end of July, stage IV in late August, stage V probably in late September, and stage VI in late fall or early winter. There is no evidence in this species of survival of stage II through the winter. Stage III, however, was obviously present during the entire year, as were stages IV and probably V. By autumn, numbers of stage III were greatly depleted, and, except for a slight increase in January (possibly rising of copepodites from deeper water), remained at a low and fairly constant level until the appearance of the new brood in late July. Stage IV fell off rapidly between late September and October, then remained at a more or less constant level until late February. This drop in numbers

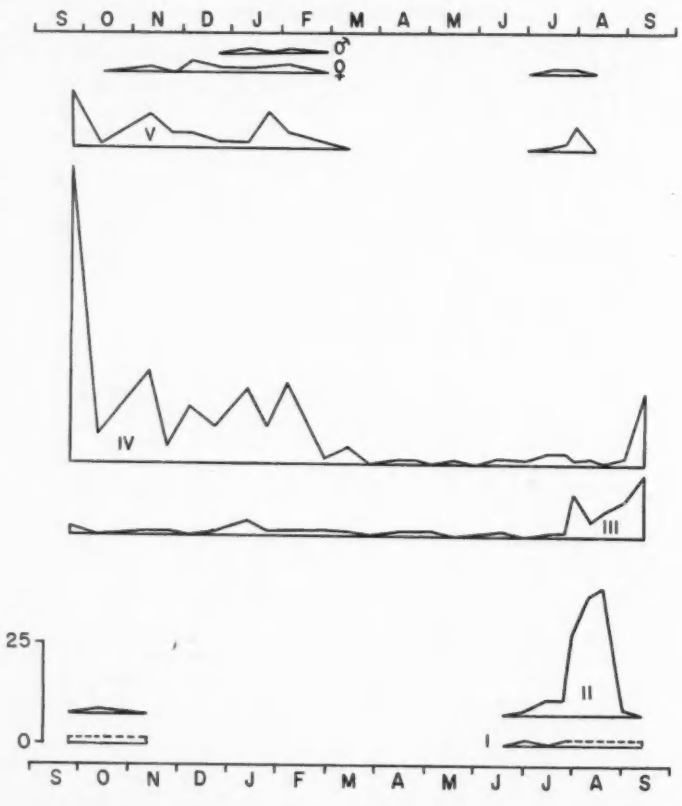

FIG. 8. Frequency of occurrence of *Calanus hyperboreus*, in number of individuals per 50-m haul, taken with the No. 0xx net. Stage I is of *Calanus* spp. combined.

probably indicated a movement to deeper water at this time, a slight numerical increase in June and July probably a return to the upper layers of previous deeper water inhabitants. Stage V disappeared from the collections in late February and reappeared in July and August. This reappearance may have been of winter-surviving stage V, of newly developed stage V

individuals, or of both. Stage VI females were present in July and from October to late February, males from early January until late February.

As in *C. finmarchicus*, development of some individuals from nauplius to stage VI occurred within a single year; others required nearly two years, and some perhaps longer. Summer development, at least as far as stage V, seems to have taken longer in the larger *C. hyperboreus* than in *C. finmarchicus*. *C. hyperboreus*, present as nauplii in early June (about 4 weeks ahead of *C. finmarchicus*) apparently did not reach stage V until at least late

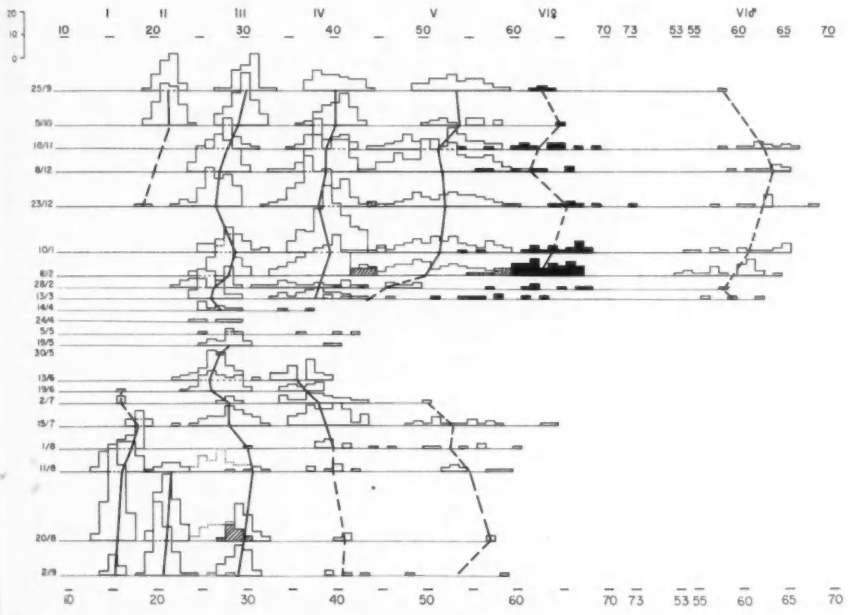

FIG. 9. Cephalothoracic length frequency histograms of stages II to VI of *Calanus hyperboreus*. Stage I is of *Calanus* spp. combined. The dotted lines show stage II of *C. finmarchicus* separated from *C. hyperboreus* on size only. The heavy lines join mean lengths of adjacent histograms. Lengths are in micrometer units (1 unit = 0.063 mm).

September, at least two weeks or possibly longer after *C. finmarchicus*, thus required at least 6 weeks longer than *C. finmarchicus* to complete a similar development. Moulting to stage VI appears to have occurred in both species, however, during late fall and winter, with the result that a single generation time, at least in some members, was completed in both species within a single year.

PSEUDOCALANIDAE

Pseudocalanus minutus (Krøyer)

This species is widely distributed in the North Atlantic, North Pacific and in adjacent seas to the north. It is known from as far north as Smith Sound (Jespersen, 1934) and to the west from Alaska and Dolphin and Union Strait (Willey, 1920), and from Hudson and James Bays (Willey, 1923; 1931).

Occurrence of stages, from I to VI, is given in Table XI and shown in Fig. 10. Nauplii appeared first in April and remained in the plankton until at least September. The first new specimens of stage I were taken first about mid-June, of stage II in early July, of stage III in mid-July, of stage IV in late July, and of stage V in late August. Whether or not any copepodites of stages I or II survived the winter cannot be determined at present. Stage III, after falling from the early September maximum until early October, decreased slowly and regularly,

TABLE XI. *Pseudocalanus minutus*. Numbers of specimens of stages I–VI per 50-m haul (No. 6xxx net), taken at Igloolik, 1955–56.

Date	I	II	III	IV	V ♀	V ♂	VI ♀	VI ♂	Total
25/9	140	110	280	400	326	804	10	0	2070
5/10	36	85	85	425	362	913	15	0	1921
10/11	0	0	50	370	289	721	7	0	1437
25/11	10	10	20	200	106	234	3	0	583
8/12	0	0	45	150	116	284	3	0	598
23/12	0	10	110	150	57	113	1	0	441
10/1	0	10	10	200	120	190	3	0	533
25/1	0	0	15	80	52	73	1	0	221
6/2	0	0	45	110	40	95	1	0	291
28/2	0	0	20	270	152	268	6	31	747
13/3	0	0	30	145	150	175	17	60	547
26/3	0	0	25	115	26	44	12	14	236
14/4	0	0	25	175	103	177	156	179	815
24/4	0	0	20	55	87	63	122	151	498
5/5	0	0	5	20	70	20	42	21	178
30/5	0	0	30	37	28	32	180	75	382
13/6	15	0	5	25	15	10	151	20	241
2/7	5	5	0	1	2	1	31	1	47
15/7	8	10	3	1	6	4	136	2	170
25/7	78	45	23	23	2	3	53	1	228
1/8	560	340	230	80	14	6	189	2	1421
11/8	525	225	250	175	19	31	81	3	1309
20/8	520	480	530	230	29	61	28	1	1879
2/9	160	640	720	640	39	131	32	7	2369
13/9	110	390	450	360	152	338	15	3	1818

except for a rise in December and a drop in January, until July. No increased spring population, comparable to what was seen in *C. finmarchicus*, was found. Stage IV too, following its early September peak, declined until July, with a conspicuous temporary numerical increase from February until April due, presumably, to additions to the population from outside the collecting area. Stage V showed a similar occurrence. Stage V males were more numerous than stage V females from late September until late April, were generally less numerous than females until near mid-August, after which time their numerical superiority returned. Females of stage VI occurred during the whole year, but in small numbers until

April. Males of stage VI appeared in the collections in February, reached maximum numbers in April, then declined, their numerical lead lost to females of stage VI at the same time as females of stage V became more numerous than stage V males. Stage VI males declined during May and June, and remained in small numbers only until September.

It appears that development from nauplii until at least stage V occurred within the first summer, from about mid-April until early August, or during a period of about 14 weeks

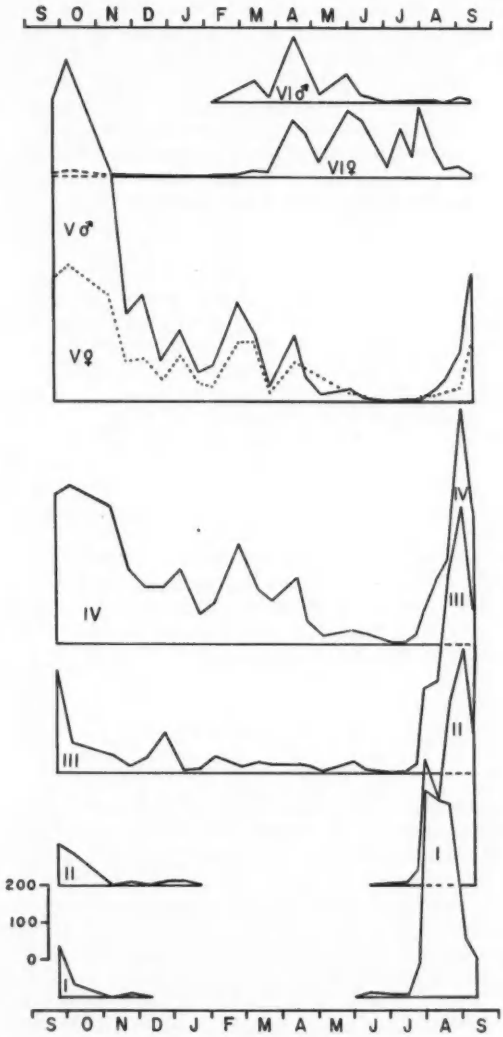

FIG. 10. Frequency of occurrence of *Pseudocalanus minutus*, in number of individuals per 50-m haul, taken with the No. 6xxx net.

(compared with about 9 weeks of *Calanus finmarchicus* and about 15 weeks for *C. hyperboreus*). In stage V a curious bimodality in females is shown in Fig. 11, lasting from September until February. The implication here is that two populations were present, presumably having moulted to stage V under different conditions of food supply, the larger one when abundant food encouraged rapid growth, the smaller one when more difficult conditions inhibited the growing rate. From this it is suggested that the larger copepodites may have reached stage V during summer, the smaller ones at some other time. The larger group, relatively scarce in September, more abundant in January, are interpreted as being the descendents of stage IV individuals which did not moult to stage V the previous autumn. They remained in stage IV during the winter, developing to stage V during the phytoplankton-rich summer period. This group may have developed from nauplii produced late in the summer of the year before, and appear to have their centre of population in deep water in autumn, rising during early winter to nearer the surface. While no clear bimodality is shown in the males of stage V, there is a suggestion especially in January and February, of a skew to the left in the histograms, perhaps indicating the existence of a similar larger, older group, only the fringe of which was sampled. These large stage V copepodites disappeared from the collections in February. The smaller stage V individuals are interpreted as having moulted to stage V at a time of food scarcity, chiefly in late fall, and as being the descendants of nauplii of the year. The fairly sudden appearance of numbers of stage VI in February was probably not a result of mass moulting at this time, but of movement to the upper water layers; similar additions to stages IV and V occurred at the same time probably in the same way. The times of production of these members of stage VI are not clear. The more than one year old (large) individuals of stage V may have moulted, perhaps in deep water, between February and summer, to produce breeding adults in spring or early summer, at the age of between one and one half and two years. The first year (small) representatives of stage V probably developed to stage VI at an age of less than one year.

The period of egg production in *P. minutus* appears to have extended over a much longer period than in *Calanus*. Ovigerous females were taken from April until August, and were found in greatest numbers in June. The first nauplii were produced before the food supply had reached abundance, and development through the first copepodite stages was slower than in *Calanus*.

In East Greenland, Ussing (1938) suggested that the life cycle of this species was almost entirely annual. Digby (1954), also in East Greenland, concluded that the species was mostly annual, but that part of the population required one and one half years to reach maturity. In Ungava Bay, Fontaine (1955) found an annual life cycle for *P. minutus*, with a small part of the population breeding a second time in late summer.

METRIDIIDAE

Metridia longa (Lubbock)

This is a common species in northern seas, found generally near the surface in arctic areas and deeper in lower latitudes. It is known from as far north as Smith Sound (Jespersen, 1934), and to the west from Dolphin and Union Strait (Willey, 1920).

Collections of this species are shown in Table XII. *Metridia* was most abundant from late November until late March, during which time the majority of specimens were caught. None occurred during April or May. One was taken in June, 20 in July, 3 in August, 6 in September and none in October or early November. The concentration of most of these individuals between November and March suggests rising to the upper water layers during this period. Stages II to VI, the latter including both males and females, were present. The small summer catch included stage I on July 2, and stages III to VI, the latter mostly males.

The taking of stage I in early July points to production of young occurring, at least partly, soon before this date, perhaps in June. The available data provide no information on the duration of stage I production, except that the finding of stage II in January suggests the

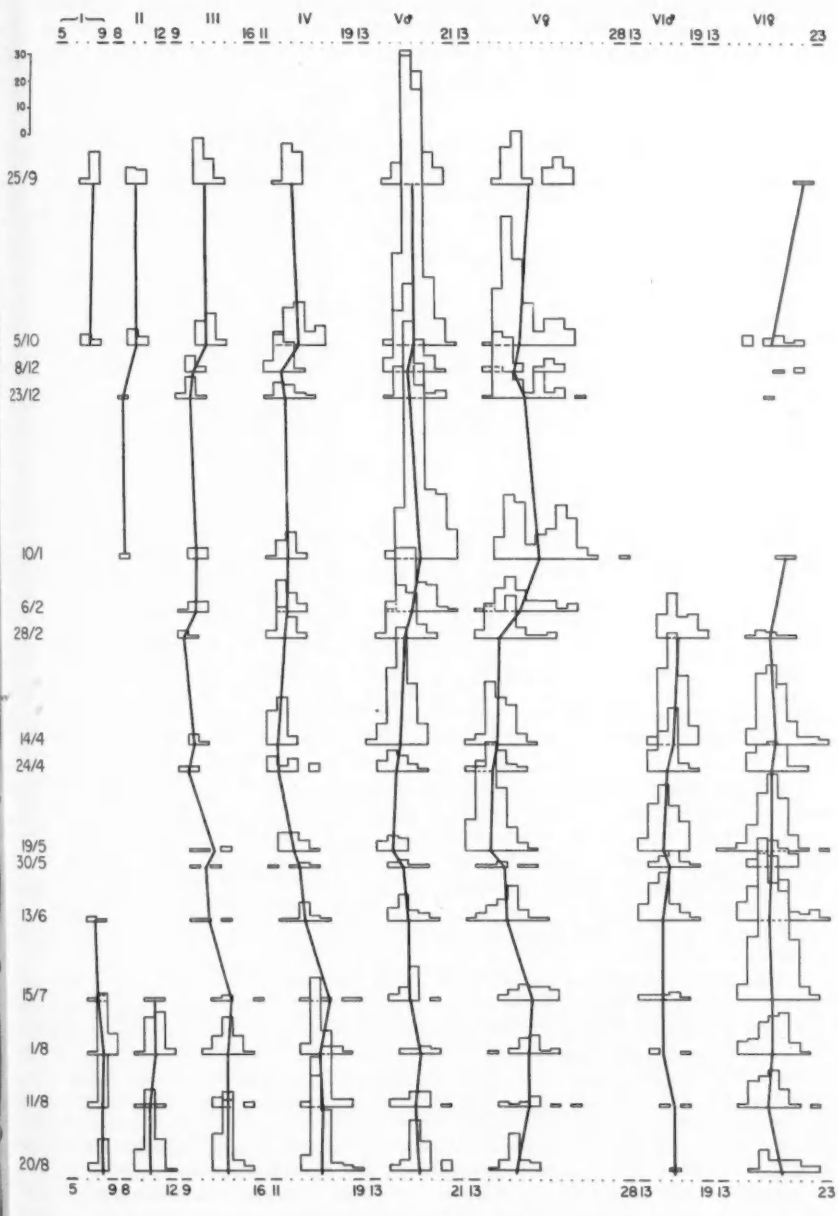

FIG. 11. Cephalothoracic length frequency histograms of stages I to VI of *Pseudocalanus minutus*. The heavy lines join mean lengths of adjacent histograms. Lengths are in micrometer units (1 unit = 0.063 mm).

possibility of continued development of stage I until early winter. Stages III and IV occurred from September until March only, stage V from November until March, and again in July and August, and stage VI (both sexes) chiefly from September until March, also in June and July. No ovigerous females were observed.

TABLE XII. *Metridia longa.* Numbers of specimens per 50-m haul (No. 6xxx net for stages I–III; No. 0xx net for stages III–VI), taken at Igloolik, 1955–56.

Date	I	II	III	III	IV	V	VI ♀	VI ♂
25/9	0	0	0	1	0	0	0	1
5/10	0	0	0	0	0	0	0	0
10/11	0	0	0	1	2	1	1	1
25/11	0	0	0	0	0	1	0	0
8/12	0	0	5	1	2	1	1	1
23/12	0	0	18	1	1	0	2	1
10/1	0	0	9	0	1	1	1	2
25/1	0	5	0	0	3	1	3	1
6/2	0	0	0	1	8	2	3	3
28/2	0	0	0	0	1	1	2	0
13/3	0	0	0	2	1	1	1	1
26/3	0	0	0	0	1	0	0	0
14/4 to 30/5	0	0	0	0	0	0	0	0
13/6	0	0	0	0	0	0	0	1
19/6	0	0	0	0	0	0	0	0
2/7	3	0	0	0	0	0	0	0
15/7	0	0	0	0	0	1	0	0
25/7	0	0	0	0	0	0	1	1
1/8	0	0	0	0	0	0	0	0
11/8	0	0	0	0	0	1	0	0
20/8 to 13/9	0	0	0	0	0	0	0	0

Eggs were probably released and nauplii produced in deep water between March and July, with development proceeding through the various stages between this time and the following spring. The species was obviously far from abundant in the Igloolik area, partly perhaps because of the limited depth of the collecting station. The small number of all stages, including adults, and the sporadic occurrence of the younger stages in the collections suggests water deeper than 50 m as the centre of population, even during the November to March period when the population appeared to inhabit not so deep water as during the rest of the year.

Both Ussing (1938) and Digby (1954) found all stages of this species more numerous in the upper waters in winter than in summer. Digby found relatively few stage I individuals, and concluded that production of nauplii probably occurred below his sampling depth of 50 m. He found stage I between May and January, and estimated development of most adults between February and July. Digby's estimate of the length of the breeding season was longer than Ussing's, who concluded that eggs were produced in August and September, and that the new generation developed during the winter. Both concluded, from East Greenland, and the present data suggest similar conclusions from Igloolik, that development does proceed during the winter, and that there is apparently less dependence upon available stocks of phytoplankton than appeared to be the case with *Calanus* and *Pseudocalanus*. The described East Greenland development of a single generation within the year, with production of young in spring, at least, appears to apply to the Igloolik *Metridia*, although more data than are at present available are required to give strict confirmation of this.

TABLE XIII. *Acartia longiremus*. Numbers of specimens per 50-m haul (No. 0xx, 6xxx and 20 nets; 6xxx in parentheses ( ), 20 as +), taken at Igloolik, 1955–56.

Date	I	II	III	IV	V	VI ♀	VI ♂
25/9	(9)	(21)	(11)	(10)	0	0	0
5/10	0	0	0	0	0	2	0
10/11	0	0	0	0	0	1	0
25/11	0	0	0	0	0	0	0
8/12	0	0	0	0	0	0	0
23/12	0	0	0	(20)	1	0	0
10/1	0	0	0	0	0	0	0
25/1	0	+	+	(5)	0	0	0
6/2	0	0	0	(15)	(15)	0	0
28/2	0	0	+	(13)	(16)	1	0
13/3	0	0	+	0	0	0	0
26/3	0	0	0	0	0	0	0
14/4	0	+	0	0	1	1	0
24/4	0	0	0	0	0	2	0
5/5	0	0	0	0	0	0	0
30/5	0	0	0	0	0	0	0
13/6	0	0	0	0	0	1	0
2/7	0	0	0	0	0	0	0
15/7	0	0	0	0	0	0	0
25/7	0	0	0	0	1	1	0
1/8	0	0	0	(15)	0	0	0
11/8	0	0	0	0	0	2	0
20/8	0	0	0	0	0	0	0
2/9	0	0	0	(14)	0	1	0
13/9	0	0	(13)	(15)	(14)	0	0

ACARTIIDAE

Acartia longiremus (Lilljeborg)

This arctic, subarctic, boreal species is circumpolar, recorded from north to Jones Sound (Jespersen, 1934), to the west from Dolphin and Union Strait (Willey, 1920), and from Hudson Bay (Willey, 1931).

A. longiremus was poorly represented in the Igloolik material, and comparatively little can be learned from the data available. Stage I (Table XIII) was found only in September, stage II in September, January and April, stage III in September, January and February, stages IV, V and VI females more frequently but sporadically throughout the year. No stage VI males were collected. The apparent total absence of adult males along with infrequent occurrence of all copepodite stages suggests a centre of distribution out of the range of the collecting station. Possibly like *Metridia longa* this species is confined principally to deeper waters than were sampled at Igloolik, and thus only a fringe of the population was sampled.

The few collections show a pattern resembling that of *M. longa*, with the suggestion of summer production of young, with progressive development through the copepodite stages possibly occurring during the winter. Absence of ovigerous females and of all adult males make probable breeding and egg production outside the area of the collecting station.

HARPACTICIDAE

Harpacticus superflexus Willey

Records of this species are few in number, from Alaska and Dolphin and Union Strait (Willey, 1920), between Greenland and Ellesmere Island (Wilson, 1936), East Greenland, Kara Sea and White Sea (Jespersen, 1939).

No. 6xxx and No. 0xx net hauls included 37 specimens, of which 32 were adult females, one was an adult male, and four were younger copepodite stages. All were taken between June 19 and September 2. The single stage VI male was 1.1 mm in cephalothoracic length,

the adult females 0.9 to 1.0 mm. This species was described by Willey (1920) and distinguished from *H. flexus* Brady by the size and shape of the finger of the second maxilliped. This structure, in the Igloolik specimens, shows excellent agreement with Willey's figure.

Oithona similis Claus

This is circumpolar, found in the North Atlantic, North Pacific and adjacent northern seas. Its records extend north to Smith Sound (Jespersen, 1934), and to the west include Dolphin and Union Strait (Willey, 1920). It is also known from Hudson Bay (Willey, 1931).

Next to *Pseudocalanus minutus* and *Calanus finmarchicus* this was probably the most abundant copepod in the Igloolik area, despite an apparent scarcity of younger copepodite stages. Table XIV gives numbers taken with the No. 6xxx net and records of occurrence in

TABLE XIV. *Oithona similis*. Numbers of specimens per 50-m haul with No. 6xxx net (No. 20 net as +), taken at Igloolik, 1955–56.

Date	I	II	III	IV	V	VI ♀	VI ♂
25/9	0	0	10	0	20	9	0
5/10	0	0	+	+	17	51	0
10/11	0	0	0	0	0	0	0
25/11	0	0	0	9	19	10	0
8/12	0	0	5	0	0	15	0
23/12	0	0	0	+	+	20	0
10/1	0	0	0	1	1	1	0
25/1	0	0	0	+	+	+	0
6/2	0	0	0	0	+	22	0
28/2	0	0	0	+	+	20	0
13/3	0	0	0	0	+	+	0
26/3	0	0	0	0	0	+	0
14/4	0	0	+	5	25	5	0
24/4	0	0	0	0	0	6	0
5/5	0	0	0	0	+	0	0
30/5	0	0	0	0	0	4	0
13/6	0	+	0	0	26	25	10
2/7	0	0	+	0	+	3	0
15/7	0	0	0	0	0	0	3
25/7	0	0	0	0	0	0	0
1/8	0	0	0	0	0	10	0
11/8	0	0	0	0	0	49	0
20/8	0	9	0	11	10	21	10
2/9	0	0	0	0	0	0	0
13/9	0	0	10	0	+	0	0

the No. 20 net on dates when the species was not recorded in the No. 6xxx net. Only a few additional occurrences are recorded from the fine than from the coarse net.

Occurrence of the copepodite stages is shown in Fig. 12. Stage I was entirely lacking from the collections. Stage II members of the new spring generation were present at least from June until August and probably the same individuals were present as stage III from July. All stages from III to VI were found throughout the year. Development of young from spring to an October peak of stage VI females suggests fairly rapid completion of a single generation cycle within a single season, these late summer–early autumn females probably producing a new generation in the following spring. Delayed development within intermediate stages probably occurred too, with achievement of stage VI not occurring until early in the spring following birth of the generation.

Digby (1954), whose material on *O. similis* from East Greenland was much more extensive than the collections from Igloolik, estimated for most individuals a single generation in the year, with development from stage I in June to stage VI in August, and possibly from stage I in September to stage VI during the period October to December. Some, Digby concluded, probably passed through two generations within a year.

ONCAEIDAE

Oncaea borealis G. O. Sars

This species ranges from the arctic to the North Atlantic, is probably circumpolar. Records extend as far north as Jones Sound (Jespersen, 1934), and include the Beaufort Sea, to the west (Johnson, 1956), and Hudson Bay (Willey, 1931).

Only adult males and females and a few members of stage V occurred in these hauls, the adults during the entire year, individuals of stage V only from May to September. From

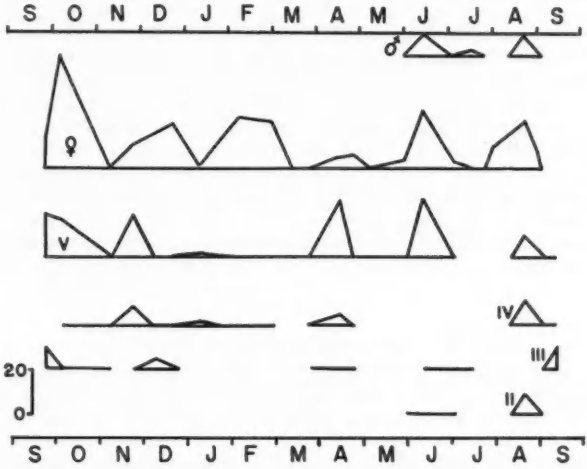

FIG. 12. Frequency of occurrence of *Oithona similis*, in number of individuals per 50-m haul, taken with the No. 6xxx net.

the apparent total exclusion of stages younger than V, it can only be assumed that production of young and development through these stages occurred outside the range of the collections. Digby (1954) found difficulty in the interpretation of stage I occurrence in his East Greenland collections, and suggested the possibility of development either below 50 m (outside the range of his nets) or outside the fjord in which he worked. It is possible that at Igloolik development through the first four stages took place in water deeper than 50 m, with introduction of only the oldest copepodites occurring at the collecting station.

Cirripedia

Larval cirripeds, mostly nauplii, towards the end of the period of occurrence partly cyprids, were taken first on May 5, and on each collection date following until September 13 (Table III). On all but two dates they were present in too small quantity to permit volumetric measurement, but on August 20 were present as 0.20 ml and on September 2 as 0.25 ml per haul (Table II). Cyprids were seen first on August 11, again on September 2 (maximum) and 13. These have not been identified to species. Thorson (1936) found *Balanus balanus* nauplii in the East Greenland plankton on June 17 and July 11, most abundantly on the later date, more than one month before the maximum production of nauplii at Igloolik. The appearance of stage II *B. balanoides* cyprids in Ungava Bay, in 1949, was recorded as August 11 (Barnes and Barnes, 1958), the period of development being given as 48 days, compared with 40 days for Halifax, N.S., and 21 to 33 days for northeastern United States. At Igloolik, the interval between the first recorded nauplii and the first cyprids was 97 days.

Amphipoda

Amphipods occurred irregularly during the year, the biomass peaks of November, April and September (Fig. 3) indicating only a few specimens of the larger species. Four species were taken, each consisting of only a few individuals. The total absence from the collections of the pelagic hyperiid *Themisto libellula* is notable, although it is possible that this active species escaped the slowly hauled nets. The species occurred in the vicinity as shown by the stomach contents of ringed seals.

Calliopiidae

Apherusa glacialis (H. J. Hansen)

This species, arctic, subarctic and circumpolar, is recorded from as far north as Smith Sound (Stephensen, 1933), to the west from Bernard Harbour (Shoemaker, 1920) and Fort Ross (Somerset Island) (Dunbar, 1942b).

A. glacialis was taken in September, November and June (Table XV). One of the large November-caught individuals (11 mm) had greatly enlarged, but empty brood pouches, suggesting recent liberation of young. The smaller June specimens (6 to 8 mm) were young amphipods, possibly produced during the preceding autumn or winter. Whether or not spawning continues into the spring cannot at present be determined. North of the Chukchi Sea, Brodskii and Nitikin (1955) found females with large eggs in November and December, with embryos in April, apparently spent in May. Young only were found in October.

Table XV. Specimens of *Apherusa glacialis* taken at Igloolik, 1955–56.

Date	Number	Length range
		mm
25/9	1	6
10/11	4	8–12
25/11	2	11–12
13/6	5	7–8
19/6	5	6–8

Gammaridae

Gammarus wilkitzki Birula

This species, arctic, subarctic, probably circumpolar, has been recorded from northern Ellesmere Island south at least to Ungava Bay (Dunbar, 1954), and from north of the Chukchi Sea (Brodskii and Nitikin, 1955).

Only 14 specimens were collected, in September, November, December and April, ranging in length from about 9 to 29 mm. No adults were found. The smallest individuals were taken in November and December, the largest in November (29 mm) and April (26 and 27 mm).

Hyperiidae

Hyperoche medusarum (Krøyer)

This is an arctic, subarctic, boreal, bipolar species, known from north to Smith Sound (Stephensen, 1933) and to the west from Point Barrow, Alaska (Shoemaker, 1955).

Fifteen specimens were collected between February and July, all immature and ranging in length from only 1.6 to 3.1 mm. The occurrence of two individuals of only 2.2 mm in February suggests recent production, and of specimens of approximately the same size from early May until late July, a lengthy spawning period extending over at least winter to early summer. The related *Hyperia medusarum* (O. F. Müller) has been found off Point Barrow,

Alaska (MacGinitie, 1955), carrying eggs in March, July and October, and to be ovigerous off West Greenland (Stephensen, 1933) in May and June.

Themisto abyssorum (Boeck)

This species is subarctic, arctic, probably circumpolar and is recorded from north to Smith Sound (Stephensen, 1933) from Alaska (Shoemaker, 1920) and from Hudson Bay (Shoemaker, 1926).

There were only 2 immature specimens in the Igloolik collections. One, nearly adult, of 13 mm, was taken on January 10, the other, probably a recently produced young amphipod, of 2.3 mm, on February 28.

Isopoda

Free-living members of the parasitic Epicaridea were taken in the plankton at various times of the year. Varying in length from about 0.5 to 0.7 mm, they are *Microniscus* stages of forms parasitic on other crustaceans.

Decapoda

Young stages only were collected in the plankton, between April and September (Table III).

Eupaguridae

Eupagurus sp.

E. krøyeri Stimpson is recorded from the North Atlantic, northern Europe, and eastern North America north to Ungava Bay, according to Squires (1957). An earlier paper however (Van Winkle and Schmitt, 1936) had reported the species from as far northwest as Fury and Hecla Strait, and the few adult eupagurids collected in 1955 and 1956 near Igloolik appear too to be of this species. Distribution is given by Squires as arctic, subarctic and boreal.

Only two specimens of *Eupagurus* larvae, each about 3.7 mm long, were taken, on April 24 and May 19. Their presence in the plankton at this time suggests the liberation of young *Eupagurus* at least as early as April. No adult Eupagurids were collected in winter or spring, hence the development of eggs could not be followed.

Hippolytidae

Very few larvae of this family were taken in the plankton. They occurred on September 25, 1955, and between May 30 and August 11, 1956. During the spring and summer lengths showed a progressive increase: May 30, 4.7 mm; June 13, 5.0–5.3 mm; July 2, 5.7 mm; July 15, 7.5 mm; August 1, 6.6 mm; August 11, 8.1 mm; September 25, 11.3 mm. Two species, at least, were represented, differing in dorso-lateral spines occurring on both the 4th and 5th abdominal segments in some and on the 5th segment only in others.

The smallest hippolytid larvae, taken on May 30, suggest the liberation of young at least as early as May, perhaps sooner. Growth of the order of 11 mm during the first summer is roughly comparable to that found in Greenland by Stephensen (1916; 1935).

Pteropoda

Limacina helicina (Phipps)

This species, of wide arctic and subarctic distribution, is recorded from as far north as Thule, Greenland (Kerswill, 1940) and to the west from northern Alaska (MacGinitie, 1955) and from Fort Ross (Somerset Island) (Dunbar, 1942b). A few young individuals only, about 1 mm in diameter, were collected, in June, July and August 1956, and in November and December 1955. No larger specimens were taken.

Clione limacina (Phipps)

This species too is widely distributed in arctic and subarctic seas, with northern American records as above.

MacGinitie (1955) reported larvae present through the winter off Point Barrow, Alaska. Only one specimen was collected at Igloolik, a young 5-mm individual, taken on March 26.

Larvacea

Oikoplura vanhoeffeni Lohmann

This species appears to have an arctic and subarctic distribution. It is recorded from Smith Sound (Kramp, 1942b) to Newfoundland (Udvardy, 1954), and to the west from between 76° and 82° n, north of the Chukchi Sea (Brodskii and Nitikin, 1955).

Specimens were collected from September until February, and in August (Table III, XVI), and were completely absent from the collections for 6 months. Table XVI gives head lengths for the individuals taken. The smallest specimens occurred in August, with the return of the species to the plankton, the largest in late September. The young apparently were produced during the period between February and August, probably in early summer, outside the range of the collections. Growth during summer evidently produced fully grown individuals by autumn and early winter. Ussing (1938) considered the closely related *O. labradoriensis* to be annual in East Greenland, with the mean spawning period occurring in May.

TABLE XVI. Specimens of *Oikopleura vanhoeffeni* taken at Igloolik, 1955–56.

Date	Number	Head length range
		mm
25/9	4	1.8–5.7
5/10	1	0.9
10/11	3	1.7–2.8
8/12	1	1.3
23/12	2	2.5
25/1	3	2.6–2.9
6/2	4	1.8–2.8
11/8	2	0.5–0.8
20/8	3	0.6–0.9
13/9	3	0.8–0.9

Fritillaria borealis Lohmann

This species is known from arctic areas and over a wide region of the North Atlantic. Its northern American records are as above.

Specimens from Igloolik were limited to August 1 to September 13, but included 446 individuals during this short time. Table XVII gives size data on the specimens. The smallest were taken in early August, when the species appeared in the plankton, after which time maximum length increased until September. The apparent absence of this species of more than 10 months presents a problem similar to that shown by *O. vanhoeffeni*. Possibly deeper water, outside the collecting area, was sought by larger individuals in winter, and breeding was undergone there, the young being produced in deep water in early summer, later rising to the depths sampled. Ussing (1938) suggested June as the principal spawning time in East Greenland.

TABLE XVII. Specimens of *Fritillaria borealis* taken at Igloolik, 1955–56.

Date	Number	Head length range
		mm
1/8	11	0.6–0.9
11/8	182	0.9–1.1
20/8	216	0.9–1.1
2/9	3	0.9
13/9	34	0.9–1.2

DISCUSSION

All the zooplankton species collected at Igloolik were formerly of known arctic occurrence. While some occupy large geographical areas, extending from arctic to at least boreal waters, and others occur predominantly in arctic and subarctic regions, none (with the possible exception of the medusa *Tiaropsis multicirrata* and the amphipod *Themisto abyssorum*) has its chief occurrence south of the arctic area. Probably all the species (again excepting *Tiaropsis*) are circumpolar; at least all have been recorded both west and east of Foxe Basin (Chukchi Sea, Beaufort Sea and Arctic Ocean, to the west; Baffin Bay and Davis Strait, to the east).

The paucity of the fauna is a characteristic of arctic regions, regarding number of species and number of higher taxonomic groups included in the plankton. Of particular significance is the reduction in the meroplankton in arctic seas, a subject discussed by Thorson (1936, 1950) and others; thus there is an increase in the relative abundance of the holoplankton in these waters. At Igloolik, the holoplanktonic species were decidedly dominant, the temporary plankton consisting almost entirely of cirriped, polychaete and decapod larvae. The number of purely holoplanktonic species too was reduced, compared with more southerly areas, and numerical dominance was taken by a small number of extremely abundant species.

Differentiation of zooplankton species into strict herbivores and carnivores cannot always be rigidly applied, because the food of some species is known to include both plants and animals, and that of others is very little or not at all known, especially in their younger stages. However, it is possible to divide the Igloolik zooplankton into those species which feed *mainly* on phytoplankton and those which feed *mainly* on zooplankton. The first group (herbivores) includes: the copepods *Calanus, Pseudocalanus, Metridia, Oithona* (Ussing, 1938), and *Acartia* (Lebour, 1922); the cirriped nauplii (Thorsen, 1946); the larvaceans *Oikopleura* and *Fritillaria* (Yonge, 1928); spionid and polynoid polychaeta larvae; and the pteropod *Limacina* (Lebour, 1922). The second group (carnivores) includes: the ctenophores (Hyman, 1940); the pteropod *Clione* (Bigelow, 1926); medusae (Hyman, 1940); the chaetognath *Sagitta*; the amphipod *Hyperia* (Lebour, 1922); and decapod larvae (Thorson, 1946).

It must be stressed that these two groups are based upon the principal food of many of the plankton species concerned, that the copepod *Calanus*, for example, may occasionally feed upon other crustaceans, including smaller copepods, and

that the smaller decapod larvae may feed upon phytoplankton material in addition to the smaller zooplankters (Lebour, 1922). The food of many of the amphipods, especially the younger stages, appears to be largely unknown. However, on the basis of this general division of feeding habits, a comparison of the frequency of the two groups in the Igloolik collections shows interesting differences. In Fig. 4 are given frequency curves for the primarily carnivorous and primarily herbivorous zooplankton, as numbers of individuals per haul, and for phytoplankton, as mean numbers of cells per litre for the four sampled depths (the latter from Bursa, unpublished). Phytoplankton production began in late April, and numbers of cells increased until mid-August. There was then a rapid decline until September, a fairly constant population at a low level until late December, then an almost complete disappearance until late April. While the curve of phytoplankton feeders (Fig. 4(b)) shows a great numerical variation between different times of the year, an abrupt summer increase beginning in July, following phytoplankton production, and a rapid early winter falling off, subsequent to phytoplankton reduction, the curve of zooplankton feeders (Fig. 4(a)) shows no comparable variation. The first group are obviously dependent largely upon phytoplankton, numbers following closely the available food supply. Individuals persisting beyond the time of abundant phytoplankton must exist largely without, or at least with a substantially reduced supply of plant food. During this period the growth rate appears to be slowed, and among the copepods, the rate of development from stage to stage much decreased. The second group, largely dependent upon the herbivores for food, find an adequate food supply during a much longer part of the year.

It was during July, August and early September when nearly all the young stages of herbivorous species were found in the plankton and when these species showed maximum concentrations. Among the herbivores this multitude of young stages was shown most clearly by the copepods *Calanus finmarchicus, C. hyperboreus,* and *Pseudocalanus minutus*. It was apparent too in the larval stages of cirripeds, in the larval polychaetes (Fig. 4(b)), and in the larvaceans. No similar concentration of young animals was found among carnivores. In contrast with the herbivores the young of the carnivorous medusae *Halitholus cirratus* appear to have been produced at least as early as March, of *Cyanea capillata* before March, of *Euphysa flammea* in March or before, and of *Aglantha digitale* perhaps during much of the winter (as well as summer). The predaceous *Sagitta elegans*, although evidently breeding chiefly during summer, may have liberated young at least as late as November, and there is evidence that among the amphipods, *Apherusa glacialis, Hyperoche medusarum* and *Themisto abyssorum* may have produced young during the winter.

Examples of widely spread reproduction times of a few other species which belong to the primarily carnivorous group may be taken from the literature. The medusa *Aeginopsis laurenti*, according to Kramp (1942a), shows no definite breeding period, hence may breed at any time during the year. Tattersall and Tattersall (1951) state that *Mysis oculata* breeds in February and March in the arctic, but give no further details. MacGinitie (1955) gives data on breeding seasons for a number of northern Alaskan invertebrates, including: the scypho-

medusa *Chrysora*, eggs and larvae, November; ctenophores, larvae, throughout the year; *Mysis oculata*, ovigerous females, October; *Hyperia medusarum*, females with eggs, July, October, March; *Erichthonius hunteri*, developing brood pouches, empty pouches, early eggs, late eggs, medium-sized embryos, fully developed embryos, February; *Eualus gaimardi*, eggs, August to October, brood recently released, October; *Clione limacina*, larvae throughout winter. Dunbar (1957) reports the amphipod *Themisto libellula* breeding in winter, possibly from September until June.

Thorson (1946) has included the factors of temperature and food supply among inducements for the spawning of marine invertebrates. Temperature has received the most attention, from a large number of workers, who have considered the factor of temperature change as a spawning stimulus. Data given in Table I and Fig. 2 show that at Igloolik the first very slight increase in surface temperature occurred on May 19, but that the first real summer warming did not begin until June. While most of the herbivorous young probably were not produced until after early June, when temperatures were rising, some (copepod nauplii) were produced before mid-May, before the first warming of even the surface water. These first apparent young of the spring were collected, however, almost simultaneously with the first evidence of spring phytoplankton development, and these, along with other phytoplankton feeders, were found in numbers (Fig. 4(b)) only during the time of phytoplankton quantity.

In East Greenland, Thorson (1936) found breeding of benthonic invertebrates (nearly all phytoplankton feeders) occurring before summer temperature rise began, and found a good correlation between animal larvae and phytoplankton occurrence. In the Sound (between Denmark and Sweden), Thorson (1946) found that the bottom animal larvae present in the plankton during the period of phytoplankton scarcity were either independent entirely of food supply or were able to feed upon small animal material. He wrote (1946, p. 424):

> "It is, however, a matter of fact that spawning on a large scale . . . sets in simultaneously with a sudden and heavy increase of the phytoplankton in the East Greenland fjords. It seems natural, therefore, to assume that there is a connection between the quantity of phytoplankton and the breeding season . . . " "There seems to be also a possibility that the temperature and the phytoplankton maximum may act together as inducements to spawning".

There is no reason to suppose that either a single factor or set of factors must necessarily act as spawning stimulii for all marine animals. It is clear, however, from the Igloolik and other observations, that there is a distinct correlation between the time of successful reproduction of plant-eating species and the presence of plant food, and evidence that the chief limiting factor upon the time of reproduction, hence of large, active populations, is food availability. Obviously, large numbers of animals which require plant food, and are liberated at a time when no plant food is available, will not survive. The same factor does not limit directly the propagation periods of carnivores, which depend not upon plants but upon the herbivores and the smaller carnivorous plankton for their food. While the young stages of the herbivores have only a limited life in the plankton, many

of the older stages are able to survive, in a relatively inactive state, presumably either without food or with a greatly reduced food supply, through the year. Thus there is a constant, if sometimes small supply of food for the carnivorous species, which with reproductive periods spread over the year, do not produce at any one time the greatly concentrated numbers of young animals found during a restricted part of the year only among the herbivores. This wider spread in the propagation times of carnivores may be, at least in part, a successful adaptation to food availability, by reduction in interspecific competition for food among the young individuals.

Comparison with Other Regions

Comparison of yearly zooplankton production at Igloolik with production in other marine areas can be made in only a crude way using data provided solely from net plankton collections. To derive figures for the Igloolik standing crop, given below, 100% efficiency of the collecting nets is assumed. This assumption is obviously erroneous, and suffices to give only minimal values. Comparison of Igloolik net yields with those from other localities is complicated further by the necessity of comparing yields from nets of different kinds.

The yearly zooplankton cycle at Igloolik exhibits many points of similarity with zooplankton cycles of East Greenland regions reported by Thorson (1936), Ussing (1938) and Digby (1953; 1954). Measurements of the standing crop at various times of the year, derived from coarse net hauls, are remarkably similar, the yearly mean at Igloolik being estimated at about 0.10 ml/m^3, in Scoresby Sound as about 0.11 g/m^3 (Digby, 1953). Comparison of maximum standing crops, at Igloolik about 0.50 ml/m^3 (September) and in Scoresby Sound about 0.59 g/m^3 (July), also shows close agreement. Expressions of mean standing crop per square metre of surface in the two localities show about 5.2 ml/m^2 at Igloolik compared to about 5.4 g/m^2 in Scoresby Sound.

Both of these arctic coastal areas appear to support a considerably smaller zooplankton population than do boreal coastal areas to the south, for example the northeast coast of the United States. These boreal waters have been shown by a number of workers to support yearly mean standing crops of about 0.4 to 0.9 ml/m^3, and of the order of 8 to 48 ml per square meter of surface; therefore in some areas at least they exceed the arctic populations by several times.

Arctic waters show a much slower rate of population turnover than do boreal seas. This may be illustrated by many species, among them *Calanus finmarchicus*, which passes through at most only a single generation and often less than a complete generation in a year at Igloolik, whereas it has at least 3 generations per year in the Clyde Sea (Marshall and Orr, 1955); and *Sagitta elegans*, with probably less than a complete generation in a year at Igloolik, and as many as 5 generations per year at Plymouth (Russell, 1932). Comparisons of zooplankton production in arctic and boreal seas would therefore be expected to differ to a still greater degree than standing crop estimates suggest, boreal zooplankton production probably exceeding arctic production by several times.

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Records of Uncommon and Unusual Fishes from Eastern Canadian Waters, 1950–1958[1]

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ABSTRACT

Records of fishes rare in Canada, and unusual occurrences of commoner ones, are presented for 65 species. First Canadian records are given for the short-nosed sturgeon (*Acipenser brevirostrum*), halfbeak (*Hyporhamphus unifasciatus*), four spot flounder (*Paralichthys oblongus*), weakfish (*Cynoscion regalis*) and striped sea robin (*Prionotus evolvans*). Specimens of unusually large size include a cunner (*Tautogolabrus adspersus*) of 17¼ inches and 3¼ lb, and a redfish (*Sebastes marinus*) of 31½ inches and 23¾ lb.

INTRODUCTION

The following notes record various species of fish that have been sent to the Biological Station, St. Andrews, N.B., in recent years. A few records fall outside the period specified, but have not been published elsewhere. Some records are new to Canada and others list additional localities for species that are caught infrequently.

The lengths given are from the tip of the closed snout to the tip of the tail in its natural position. Specimens that are marked with an asterisk (*) are preserved in the Museum at the Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B.

We wish to thank Mr W. C. Schroeder, Museum of Comparative Zoology, Cambridge, Massachusetts; Dr R. H. Backus, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts; Dr C. M. Breder, American Museum of Natural History, New York City, and Dr W. B. Scott, Royal Ontario Museum of Zoology, Toronto, Ont., for assistance with identifications. Many fishermen, fishery officers, and others have contributed specimens. Thanks are due to Dr W. R. Martin, Dr F. D. McCracken, Dr M. W. Smith, Mr Murray Fraser, Mr R. MacPherson, Mr E. G. Sollows, and Mr G. J. W. Sullivan of the staff of this Station and to Dr W. J. Dyer of the Technological Station, Halifax, N.S., for facilitating the transfer of specimens and information. Others are mentioned at appropriate places in the notes.

A few records are from a manuscript report by Mr D. H. Steele; these are from the northern Gulf of St. Lawrence region (Steele, 1958).

NOTES ON SPECIES

Carcharodon carcharias (Linnaeus) White Shark

A specimen, 260 cm (8½ ft) long, was caught in a weir, operated by Mr Ellis Mawhinney, at Maces Bay, N.B., on August 3, 1954.

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Cetorhinus maximus (Gunnerus) BASKING SHARK

Several specimens have been examined or reported. (1) A 500-cm (16½-ft) specimen was caught in a weir at Maces Bay, N.B., September 21, 1934. (2) A 425-cm (14-ft) specimen was found at East Bathurst, N.B., in late August 1952. It was identified by a Fishery Officer and reported by Mr J. S. MacPhail. (3) A 365-cm (12-ft) specimen was caught off Devils Island, N.S., August 27, 1953. Identified by Dr W. J. Dyer. (4) An 870-cm (28½-ft) specimen at Maces Bay, N.B., September 13, 1953. Identified by Dr H. D. Fisher. (5) A 365-cm (12-ft) specimen caught off Apple Tree Cove, Lunenburg County, N.S., in August 1953. Newspaper account only. (6) A 730-cm (24-ft) specimen caught in a weir operated by Mr Percy Simpson, Green Cove, near Letite, N.B., July 29, 1954. (7) A 2550-cm (40-ft) specimen caught at the southern end of Grand Manan, N.B., in July 1958. Newspaper account.

Prionace glauca (Linnaeus) BLUE SHARK

This shark was observed frequently in St. Margaret Bay, N.S., in the summer of 1951 by one of the authors (L.R.D.). A 150-cm (5-ft) specimen was identified by Dr L. P. Chiasson, St. Francis Xavier University, Antigonish, N.S. It was caught near Miminegash, P.E.I., in 1952.

Sphyrna zygaena (Linnaeus) HAMMERHEAD SHARK

Reported from St. Margaret Bay, N.S., in July 1951, where it was identified by one of the authors (L.R.D.).

Raja senta Garman SMOOTH-TAILED SKATE

A specimen, 27 cm (10½ in) long, was caught in 50 fathoms, 9 miles north of Digby, N.S., July 28, 1951. Dr J. C. Medcof brought in the specimen. Taken frequently in the neighbourhood of Fox River, P.Q., in 1953 and 1954 (Steele, 1958).

Hydrolagus affinis (Brito Capello) CHIMAERA

A specimen, 109 cm (43 in) long, was caught in early June 1958, in deep water, possibly up to 750 fathoms, off the southwest corner of St. Pierre Bank at Lat. 44°47′ N, Long. 55°56′ W. It was taken by the vessel *Harry B. Nickerson III*, Captain Warren S. Levy. The specimen is now in the collection of the Royal Ontario Museum of Zoology, Toronto, Ont.

**Acipenser brevirostrum* LeSueur SHORT-NOSED STURGEON

A specimen, 69 cm (27 in) long, was caught by the M.V. *Harengus* in the Long Reach, Saint John River, N.B., on May 20, 1957. Identification is by Dr V. D. Vladykov. A paper on this specimen is in preparation; it represents the first authenticated record of the species in Canada.

Tarpon atlanticus (Cuvier and Valenciennes) TARPON

A small tarpon was brought in to the Technological Station in Halifax, N.S., in 1947. The identification was confirmed by one of the authors (A.H.L.). Two specimens, 122 and 168 cm (4 and 5½ ft) long, were caught near Sambro, N.S., on August 3 and 4, 1953. They were identified by Dr W. J. Dyer; a newspaper photograph was published.

Etrumeus sadina (Mitchill) ROUND HERRING

Small numbers were present in Passamaquoddy Bay in August and September, 1952. A few were seen in Deer Island weirs in October 1953. Several hogsheads were caught in Mr J. McGowan's weir at Maces Bay, N.B., on September 3, 1958.

Brevoortia tyrannus (Latrobe) MENHADEN

A 13-cm (5-in) specimen* was taken in a midwater trawl operated from the M.B. *Mallotus* near Hagartys Cove, Maces Bay, N.B., on February 8, 1952. A larger specimen, 37 cm (14½ in) long, was caught in a weir at Digdeguash, N.B., on June 23, 1954, and others were reported.

**Salmo gairdneri* Richardson STEELHEAD TROUT

A sea-run specimen, 44 cm (17 in) long, was caught in a trap at Wilmot Brook, P.E.I., on September 17, 1958. Other specimens were also seen. This species occurs in fresh water where it is known as "rainbow trout". It has not been known to be sea-run in the Maritime Provinces before. This information was supplied by Dr M. W. Smith.

Coregonus clupeaformis (Mitchill) WHITEFISH

Whitefish have been caught at a number of points in the sea in the Maritime Provinces. A 51 cm (20¼ in) specimen was caught at a wharf at Wedgeport, N.S., on July 8, 1954. Mr W. L. Klawe, who forwarded the specimen, reported seeing seven others. A 29 cm (11½ in) specimen was caught in a herring weir at Halls Harbour, N.S., on May 31, 1958. A 44 cm (17 in) one was caught in a weir near Blacks Harbour, N.B., in June or July 1958.

The species has also been found in two fresh water localities, viz. Millipsigate Lake, Lunenburg County, N.S., where five specimens from 48 to 54 cm (19 to 21¼ in) long were caught in August 1955; and a 32 cm (12⅝ in) specimen was caught by the M.V. *Harengus* in the Long Reach, Saint John River, on August 28, 1957.

Identification of all these whitefish was confirmed by Dr W. B. Scott, Royal Ontario Museum of Zoology.

Argentina silus Ascanius ARGENTINE

Specimens were taken on the Banks off Nova Scotia by the steam trawler *Venosta* in early January 1951. They were identified by Dr W. J. Dyer.

Two partially digested specimens, about 36 cm (14 in) long, were taken from the stomachs of swordfish that were harpooned in the Browns-Georges Bank area in the summer of 1952. Stomachs from the same area, examined in 1953, contained larger numbers of argentines.

**Lampadena braueri* Zugmayer LANTERNFISH

Specimens were found in the stomachs of swordfish that were caught between Browns and Georges Banks in the summers of 1952 and 1953. Digestion had damaged the photophores. Dr R. H. Backus examined them and reports the identification as probably correct.

**Myctophum humboldti* (Risso) LANTERNFISH

A specimen, 13 cm (5 in) long, was dipped at the surface at night by Mr W. B. Bailey on C.N.A.V. *Sackville* at Lat. 42°51′ N, Long. 61°44′ W, November 10, 1952. It was identified by Dr Backus.

**Myctophum punctatum* Rafinesque LANTERNFISH

A 12-cm (4¾-in) specimen was caught by the trawler *Cape Argus* on the Grand Banks at Lat. 43°30′ N, Long. 51°00′ W, in 80 fathoms on January 4, 1954. It was forwarded by Mr Murray Fraser. Identification confirmed by Dr Backus.

Cyclothone microdon (Günther) SMALL-EYED LANTERNFISH

Two small specimens, about 6 cm (2½ in) long, were caught in the Fox River, P.Q., area by the M.V. *J. J. Cowie* in 110 fathoms. Identified by Steele (1958).

Notacanthus nasus Bloch SPINY EEL

The spiny eel is caught frequently on the Grand Banks. Many of the specimens and records have been forwarded by Dr W. J. Dyer. (1) Specimens from the Grand Banks, December 1950. (2) Four were caught at Lat. 43°16′ N, Long. 51°20′ W, by the trawler *Fort Louisburg* on March 14, 1953. A 72-cm (28¾-in) specimen from these was sent in by Mr R. MacPherson. (3) An 81-cm (32-in) specimen from the Grand Banks was caught by the trawler *Cape Smoky* in July 1953. (4) An 89-cm (35-in) specimen was caught on the western edge of the Grand Bank at Lat. 44°24′ N, Long. 52°54′ W, in 160 fathoms, in early February 1955; it was sent in by Mr Murray Fraser. (5) Specimens, 75 and 99 cm (29½ to 39 in) long, were caught on the southern edge of the Grand Banks and elsewhere on the Bank in 70 fathoms by the trawlers *Cape Alert* and *Acadia Snowbird*.

Conger oceanica (Mitchill) CONGER EEL

A specimen in the "leptocephalus" stage was taken by a plankton net operated from C.N.A.V. *Sackville*, August 20, 1954, on Lahave Bank at Lat. 43°05′ N, Long. 64°10′ W. Identification was confirmed by Mr Wm. C. Schroeder. Another specimen caught in Passamaquoddy Bay on July 11, 1956, differs in pigmentation and position of the finfold and is included here provisionally.

Gymnothorax funebris Ranzani MORAY EEL

A specimen, 169 cm (67 in) long, was caught and kept alive at a wharf at Eastern Passage, Halifax Harbour, N.S., on August 30, 1952. It was turned over to Mr G. J. W. Sullivan. The identification was confirmed by Dr W. B. Scott and the specimen is retained in the Royal Ontario Museum of Zoology.

Alepisaurus ferox Lowe LANCETFISH

Captain Alexander Nickerson of Lockeport, N.S., caught three specimens of this fish off Lahave Bank in 210 to 700 fathoms of water on August 22, 1953. Dr F. D. McCracken examined one, 148 cm (58 in) long, and confirmed the identification.

**Hyporhamphus unifasciatus* (Ranzani) HALFBEAK

A specimen, 19 cm (7½ in) long, was caught in a herring weir at Chamcook, N.B., on September 30, 1949. This is the first record for the Canadian Atlantic coast.

Paralepis rissoi krøyeri Lütken SCALED LANCET

A number of specimens, some about 24 cm (9½ in) long, were caught in 1953 and 1954 by the M.V. *J. J. Cowie*, by trawling and from the stomachs of redfish. They were caught in the neighbourhood of Fox River, P.Q., and between Cap de la Madeleine and Bonaventure Island. Identified by Steele (1958).

**Cypselurus furcatus* (Mitchill) FLYING FISH

A specimen, 18 cm (7 in) long, was taken in a trap at Northwest Cove, St. Margaret Bay, N.S., in the summer of 1951. It was identified by Dr C. M. Breder of the American Museum of Natural History, New York.

Paralichthys dentatus (Linnaeus) SUMMER FLOUNDER

One specimen, 52 cm (20½ in) long, was captured by the M.B. *Evelyn Francis*, Captain James Calder, in Passamaquoddy Bay, N.B., December 3, 1955. This is the second Canadian record, it was earlier reported by Günther (1880) from Lahave Bank.

**Paralichthys oblongus* (Mitchill) FOUR SPOT FLOUNDER

This species has not been reported from Canadian waters previously. Two specimens were found in 1958. The first, 37 cm (14½ in) long, was trawled in Passamaquoddy Bay, N.B., on June 7, 1958, by the M.B. *Campobello*, Captain J. Fitzgerald. A second specimen, 43 cm (17 in) long, a record size, was trawled in the lower Bay of Fundy in early July 1958. It had six spots.

Zenopsis ocellata (Storer) JOHN DORY

Only small specimens have been seen. One*, 9 cm (3½ in) long, was caught in a weir at Herring Cove, Campobello Island, N.B., in early October 1942. It had a juvenile colour pattern of small dark spots (Fig. 1).

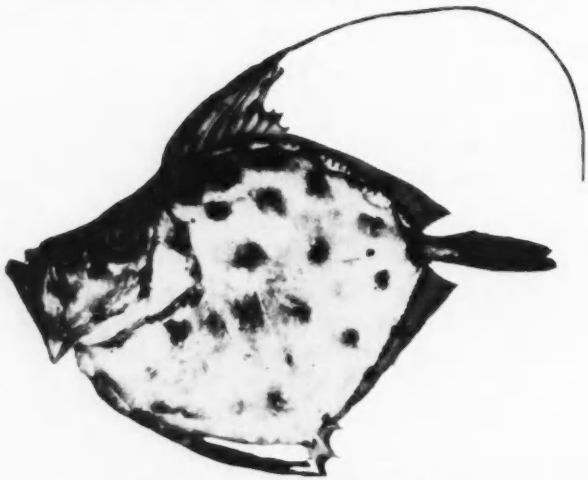

FIG. 1. Photograph of *Zenopsis ocellata* (Storer), taken at Herring Cove, Campobello Island, N.B., October, 1942. Length 9 cm.

Another young specimen*, 11 cm (4¼ in) long, was caught on August 19, 1958, by the M.V. *Harengus* off the western end of Sable Island Bank at Lat. 42°58′ N, Long. 61°56′ W, in about 100 fathoms of water.

A third specimen, 18½ cm (7¼ in) long, was caught on March 1, 1959, on Lahave Bank at Lat. 43°20′ N, Long. 64°10′ W, in 40 to 50 fathoms; caught by the trawler *Beothuk*, Captain Chas. Leary. It shows the juvenile spots faintly.

Fistularia tabacaria Linnaeus TRUMPET FISH

A specimen was taken in St. Mary Bay, N.S., in September 1952. Its length was 44 cm (17¼ in) to the tip of the caudal fin. This record was earlier credited erroneously to St. Margaret Bay (FRB, 1953, p. 50).

**Pneumatophorus colias* (Gmelin) CHUB MACKEREL

Two specimens, about 22 cm (8½ in) long, were caught in St. Margaret Bay, N.S., in September 1952.

Sarda sarda (Bloch) COMMON BONITO

A specimen was taken at Ketch Harbour, N.S., on September 27, 1950; another*, 27½ cm (10¾ in) long, was found at Centre East Pubnico, N.S., September 12, 1951; large numbers from 35 to 39½ cm (13¾ to 15¾ in) in length, were taken in traps in St. Margaret Bay, N.S., in September 1952.

Ruvettus pretiosus Cocco ESCOLAR

A specimen, 110 cm (43 in) long, was caught by the schooner *Dot and Hellie* in 300 fathoms, near Sable Island Bank at Lat. 43°22′ N, Long. 60°32′ W, on September 26, 1952. It is now in the collection of the Royal Ontario Museum of Zoology.

Benthodesmus atlanticus Goode and Bean

A specimen was taken by the trawler *Venosta* in January 1951, 120 miles east southeast from Sambro Lightship, on Sable Island Bank, in 90 fathoms.

Coryphaena hippurus Linnaeus DOLPHIN

Three specimens, each about 35 cm (14 in) long, were caught by gill net off North Rustico, P.E.I., in the summer of 1945. They had been split and salted. They were identified by Dr John T. Nichols, American Museum of Natural History, New York.

Another specimen was reported by Dr W. J. Dyer as having been caught off Nova Scotia in 1952.

Palinurichthys perciformis (Mitchill) BARRELFISH

A 28-cm (11-in) specimen was taken in a trap net at St. Margaret Bay, N.S., August 29, 1951.

A 30-cm (11¾-in) specimen was found near Ryders Ledge Buoy, between Cape Sable and Bon Portage Island, N.S., August 25, 1958. It was forwarded by Fisheries Officer J. E. Daley.

**Naucrates ductor* (Linnaeus) PILOTFISH

A specimen, 28 cm (11 in) long, was taken off Halifax, N.S., in late July 1949. Another, 33 cm (12¾ in) long, was caught by the M.V. *Harengus* while fishing each of Georges Bank at Lat. 41°06′ N, Long. 64°12′ W, on July 20, 1955.

**Seriola zonata* (Mitchill) BANDED RUDDERFISH

A specimen, 19 cm (7½ in) long, was caught west of the Canso Causeway, N.S., in October 1955. It was sent in by Mr Martin C. Boston of Port Hawkesbury, N.S.

**Vomer setapinnis* (Mitchill) MOONFISH

A specimen, 5 cm (2 in) long, was caught in St. Margaret Bay, N.S., in September 1952.

Pomatomus saltatrix (Linnaeus) BLUEFISH

There are several records: (1) *One, about 35 cm (13¾ in) long, was taken at Ketch Harbour, N.S., on September 16, 1950. (2) *A specimen, 35½ cm (14 in) long, was caught in Minas Basin, N.S., in a weir between Five Islands and Bass River in mid-July 1951. (3) Several specimens*, from 13 to 17 cm (5 to 6½ in) long, were taken in St. Margaret Bay, N.S., in September 1952. (4) A specimen, 35 cm (13¾ in) long, was caught in a weir at Black Rock, Kings County, N.S., on August 12, 1957.

Stenotomus versicolor (Mitchill) SCUP

A specimen, about 20 cm (8 in) long, was caught by the M.V. *J. J. Cowie* while flounder fishing in St. Mary Bay, N.S., September 29, 1950. The same boat caught a 24-cm (9½-in) specimen* in Passamaquoddy Bay, N.B., December 10, 1954. Another of similar size was caught by the dragger *Donna Louise* on Sable Island Bank on April 2, 1955. A 30-cm (11¾-in) specimen was caught in a weir at Harbourville, Kings County, N.S., in July 1955, by Mr Oscar Banks.

**Cynoscion regalis* (Bloch and Schneider) WEAKFISH

A specimen, whose body, minus the head, measured 37 cm (14½ in) in length, was caught in a weir at Economy, Minas Basin, N.S., about September 7, 1955. It was sent in by Fishery Officer J. B. Fleury of Truro, N.S. Identification was confirmed by Mr Wm. C. Schroeder. This is the first definite record for Canadian Atlantic waters.

Lopholatilus chamaeleonticeps Goode and Bean TILEFISH

A specimen, about 75 cm (29½ in) long, was caught in 78 fathoms between Lahave and Emerald Banks on June 2, 1953. Sent in by Mr Murray Fraser. A second specimen*, 89 cm (35 in) long, was caught on May 1, 1954, in the same area at Lat. 43°21′ N, Long. 64°40′ W, in 85 fathoms of water. It was caught by the *Clarence and Walter*, Captain Alexander Nickerson of Lockeport, N.S.

**Sebastes marinus* (Linnaeus) REDFISH

A record size of redfish was caught on August 13, 1958, offshore from Emerald Bank in 275 fathoms at Lat. 42°38′ N, Long. 62°56′ W. The specimen is 80 cm (31½ in) long and weighs 23½ pounds. It was caught by Captain Russell Decker.

**Artediellus uncinatus* (Reinhardt) HOOK-EARED SCULPIN

A specimen, 7 cm (2¾ in) long, was caught in a beam trawl by the M.B. *Clupea H.* near Clam Cove Head, Passamaquoddy Bay, N.B., on August 26, 1952.

**Triglops ommatistius* Gilbert MAILED SCULPIN

A specimen, 10 cm (4 in) long, was caught in 40 fathoms off Kempt Head, Great Bras d'Or, N.S., on August 3, 1950. It was caught by Dr D. M. Scott, University of Western Ontario, London, Ont.

Cottunculus microps Collett ARCTIC SCULPIN

A 12½-cm (5-in) specimen was caught by the M.V. *J. J. Cowie*, 3 miles east of Fox River, P.Q., in 117–119 fathoms, on June 22, 1954. Identified by Steele (1958).

Aspidophoroides monopterygius (Bloch) ALLIGATORFISH

A juvenile specimen, 23 mm (1 in) long, was taken in a surface plankton tow about 5 miles off Richibucto Head, N.B., on June 18, 1952. The pectoral fins were long and black-tipped.

Leptagonus decagonus (Bloch and Schneider) NORTHERN ALLIGATORFISH

A specimen, about 20 cm (8 in) long, was caught on Orphan Bank in the Gulf of St. Lawrence, in late August 1952, by the dragger *Little Gaspé*. Another*, of similar size, was caught by the M.V. *J. J. Cowie* off Fox River, P.Q., in 160 fathoms, on October 20, 1953. A smaller specimen, 13 cm (5 in) long, was taken off Margaree Harbour, N.S., in the summer of 1953 by the dragger *Marion Crouse*.

**Careproctus longipinnis* Burke SEA TADPOLE

Six specimens were taken by the M.V. *J. J. Cowie*, in 1953, off Fox River, P.Q., and west of Baie Comeau, P.Q.; in 1954 fourteen more were caught off Fox River. Identified by Steele (1958).

Prionotus carolinus (Linnaeus) COMMON SEA ROBIN

A specimen was caught at Harbour du Loutre, Campobello, N.B., in October 1938. Another* was sent in from southwestern Grand Manan, N.B., in September 1951. A specimen, 31 cm (12¼ in) long, was caught in a weir at Sandy Cove, Digby County, N.S., on August 14, 1954. It was found by Mr Arnold Banks. Another, 35 cm (13¾ in) long, was caught by the M.V. *Industrial II*, 10 miles northwest from Digby Gut, N.S., December 2, 1955; only a drawing and description seen in this case.

**Prionotus evolans* (Linnaeus) STRIPED SEA ROBIN

Three specimens were found in the lower Bay of Fundy in 1957. A 26-cm (10¼-in) specimen came from Harbour du Loutre, N.B., where it was caught September 13, 1957. A 28-cm (11-in) specimen was caught near Leonardville, Deer Island, N.B., on October 4, 1957, and a 31½-cm (12⅜-in) specimen was taken among the Murr Ledges, November 30, 1957. The latter was sent in by Fishery Officer J. F. Gilmore. These are the first Canadian Atlantic records.

**Tautogolabrus adspersus* (Walbaum) CUNNER

A record sized, male specimen, 44 cm (17¼ in) long and weighing 3¼ pounds, was caught off Head Harbour, Campobello, N.B., September 9, 1953.

Tautoga onitis (Linnaeus) TAUTOG

A sport fishery for this species developed suddenly in Eel Brook Lake, a salt water lake in Yarmouth County, N.S. About 2000 fish were caught in 1957 and about 450 in 1958. Mr E. G. Sollows, of the Fisheries Research Board's Staff, supplied this information and provided a typical specimen* that is 43 cm (17 in) long.

Remora brachyptera (Lowe) SWORDFISH SUCKER

The crew of the M.V. *J. J. Cowie* found one* of these fish attached to a *Mola mola* that was harpooned at Ketch Harbour, N.S., in September 1950. It was 24 cm (9½ in) long. A specimen about 12 cm (4¾ in) long, was found adhering to a swordfish that was harpooned between Georges and Browns Banks in the summer of 1952.

Remora remora (Linnaeus) REMORA

A specimen was reported off Nova Scotia in 1952 by Mr Murray Fraser.

A specimen*, 23 cm (9 in) long, was caught by the trawler *Cape Bonnie*, southwest of Sable Island in August 1958. It was sent in by Dr W. J. Dyer.

Cryptacanthodes maculatus Storer WRYMOUTH

A 61-cm (24-in) specimen was caught off Katys Cove, Passamaquoddy Bay, N.B., by the M.V. *J. J. Cowie* on November 10, 1950.

**Lycodes vahli maculatus* Vladykov and Tremblay VAHL'S EELPOUT

The M.V. *J. J. Cowie* took 17 specimens in 1953 between the mouth of the Saguenay River and Seven Islands, P.Q., and off Fox River and Port Menier, P.Q. Over 100 specimens were caught off Fox River in 1954. Identified by Steele (1958).

Melanostigma gelatinosum Günther

Five specimens were taken in 1953 east of the mouth of the Saguenay River, P.Q., and two specimens were taken off Fox River, P.Q., in 1954. Identified by Steele (1958).

Balistes carolinensis Gmelin TRIGGERFISH

A specimen* was taken off Halifax, N.S., in late July 1950. A 28-cm (11-in) specimen was caught 5 miles off Port Bickerton, N.S., by Mr Reginald Kaiser on September 4, 1956; a 35½-cm (14-in) specimen was caught at Rocky Bay, Richmond County, N.S., by Mr James Keating on September 24, 1956. A 36-cm (14-in) specimen* was caught 15 miles southeast of Devils Island, N.S., September 26, 1957. These specimens were sent in by Dr W. J. Dyer.

Monacanthus hispidus (Linnaeus) FILEFISH

Specimens were received from Ketch Harbour*, N.B., September 11, 1950; from Wilson's Beach*, N.B., September 27, 1950; and from Shelburne, N.S., September 28, 1950, that were probably this species.

A specimen, 12 cm (4¾ in) long, was caught near Lockeport, N.S., in late August 1953, and forwarded by Mr W. L. Klawe.

**Alutera schoepfi* (Walbaum) ORANGE FILEFISH

A specimen, 46 cm (18 in) long, was caught in a herring net at Peggys Cove, N.S., August 23, 1955. Caught by Mr Edward Morash, it was forwarded by Dr W. J. Dyer.

**Sphaeroides maculatus* (Bloch and Schneider) PUFFER

A specimen was caught at Kingsport, N.S., in July 1951. Only the skeleton was available for examination.

Mola mola (Linnaeus) SUNFISH

One was harpooned off Halifax, N.S., on August 4, 1950. Another weighing 300 pounds, was harpooned at Ketch Harbour, N.S., by the crew of the M.V. *J. J. Cowie* in September 1950. One, weighing 500 pounds, was reported from Chance Harbour, N.B., August 16, 1951, (photograph in Saint John Telegraph–Journal). Unusual numbers were caught in trap nets in St. Margaret Bay, N.S., in 1951.

Lophius americanus Cuvier and Valenciennes ANGLER

A specimen, 91 cm (36 in) long, and weighing 12 pounds, was handlined off North Rustico, P.E.I., on August 4, 1952. It was reported by Fishery Officer L. D. Darrach.

**Ceratias holbölli* Krøyer DEEP SEA ANGLER

A 24-cm (9½-in) specimen was caught by the trawler *Cape Spry* on July 7, 1958, east of Anticosti Island at Lat. 49°10′ N, Long. 60°20′ W. Sent in by Mr R. MacPherson.

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Vernal and Hiemal Races among Anadromous Fishes[1,2,3]

By L. S. Berg

(*Translated by W. E. Ricker*)

TRANSLATOR'S PREFACE

The paper to follow is one of the most interesting of the numerous scientific contributions of the late geographer and ichthyologist L. S. Berg, a member of the Academy of Sciences of the USSR. It marks the first attempt to bring together scattered information concerning intra-specific seasonal groups among anadromous fishes: that is, groups differentiated in respect to the time of their approach to fresh water and the time of their spawning. These seasonal races, as Berg calls them, occur in quite a variety of fishes, including a number of the important commercial fishes of Canada. A recognition of their existence is of profound importance both for fish-cultural procedures and for management policies. On the other hand, these seasonal races (often called *runs* in America) are not necessarily the smallest recognizable unit within a species: each seasonal group can, in a large river, be made up of a number of individual *stocks* associated with specific tributaries.

Many additional examples of seasonal runs have been described since 1934, in the old world and in the new. In fact it now appears that Berg's treatment must be broadened, because more than two seasonal runs have been recognized among anadromous fish in certain rivers. In the Sacramento, for example, three rather distinct groups of stocks of *Oncorhynchus tshawytscha* are recognized — the spring chinooks, fall chinooks and winter chinooks. Similarly Driagin (in *Doklady Akademii Nauk SSSR*, 71: 785–788, 1950), basing his distinctions partly on the fish's reaction to injections of pituitary extract, has recognized no less than four "races" of *Acipenser güldenstädti* in the Kura River—named early vernal, late vernal, summer-arriving hiemal and autumn-arriving hiemal; the first two spawn during the year of arrival, the last two winter over and spawn the following spring.

Such examples suggest that although Berg's analogy with the cereal grains is interesting, no attempt should be made to force all known stocks of anadromous fishes into one or other of the two categories vernal and hiemal. The various examples quoted by Berg, taken with those described since 1934, exhibit almost every conceivable combination of season of arrival, season of spawning, and length of stay in fresh water before spawning.

Professor Berg's introduction to the subject of seasonal races is of such wide interest that it is profitable to make an English translation available, even 25 years after its original publication. A few footnotes have been added to clarify the English text; these and other interpolations are put in square brackets.

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[1]Original title: Yarovye i ozimye rasy u prokhodnykh ryb. Published in *Izvestiia Akademii Nauk SSSR, Otdel Matematicheskikh i Estestvennykh Nauk*, for 1934, No. 5, pp. 711–732.

[2]Fisheries Research Board of Canada, Translation Series, No. 206.

[3][The words here translated as "vernal" and "hiemal" are *yarovoi* and *ozimyi*, respectively, words which are primarily used with reference to agricultural crops. The adjectives *vesennii* and *zimnii* are translated as "spring" and "winter", respectively. The distinction is necessary in order to avoid confusion of the various kinds of races described, particularly as some of Berg's "hiemal" races enter the river as early as the late spring or summer previous to the year of spawning, while others do not arrive until early spring of the year of spawning; and the "vernal" races variously enter in late spring, summer, or even in autumn. This distinction is maintained in the translation even throughout the comparison with cereal grains in the Discussion, where the usual English equivalents of *yarovoi* and *ozimyi* would be "spring" and "winter" (wheat, etc.).

The Russian word *rasa* is translated as "race", but the text makes it clear that there are not *necessarily* any systematic, taxonomic or genetic implications attached to this term as Berg uses it.]

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[INTRODUCTION]

DIADROMOUS FISHES are defined as those which, for reproduction, leave the environment to which they are accustomed and migrate from salt water to fresh water or, conversely, from fresh water to salt. The eel, *Anguilla anguilla* (L.), belongs to the latter category; for reproduction it goes out of the rivers and down to the depths of the ocean. All other diadromous fishes leave salt walter and go into fresh water for spawning; to this group belong many representatives of the lamprey, sturgeon, herring, salmon and carp families[4].

It is noteworthy that anadromous fishes are peculiar to the temperate and to some extent the polar latitudes of both hemispheres[5]; the tropics lack them.

One of the most puzzling phenomena of fish biology is the occurrence among many anadromous fishes of two forms or races, which are distinguished from one another by their times of entry into the river from the sea for spawning or, more exactly, by the time when these fish (while in the sea) receive the impulse to enter the river for spawning. Such races can be called *seasonal* races.

Seasonal races also exist among non-anadromous fishes; they are especially clearly developed among, for example, the sea herring, *Clupea harengus*. But in the present article we will discuss seasonal races of anadromous fishes only.

SALMON FAMILY

The best studied seasonal races are found among fishes of the salmon family. They are especially clearly and simply developed in one of the Pacific salmon, *Oncorhynchus keta* [the chum or keta salmon], with which species we will begin our exposition.

On the Amur River the chum salmon are divided into *summer* keta and *autumn* keta. The migration of the summer keta from the sea into the Amur begins in the first days of July and usually ends at the time the autumn run begins—about the middle of August. In consequence [page 712] the summer keta arrive on the spawning grounds a month earlier than the autumn; their spawning takes place about the middle of August, while that of the autumn keta begins in the middle of September. The summer keta does not ascend the river as far as does the autumn keta: it reaches the confluence of the Ussuri River and enters that river in small numbers, whereas the autumn keta goes much farther upstream, as far as Zabaikalia [the region near Lake Baikal]. Now let us observe an extremely important fact, noted by V. K. Soldatov (1912, p. 137): *the autumn keta arrives from the sea with its sexual products in a much less advanced state of development than what is observed among the late individuals of the summer keta that are migrating at the same time*. For example, among 20 late-arriving summer keta caught in the Amur estuary from August 24 to September 1, 1907, the weight of the eggs averaged 13.7% of the total body weight, while among 63 autumn keta taken at the same time it averaged 5.6%.

[4][Fishes of this latter sort are usually called *anadromous* in English. This more familiar word will be used from here on to translate "prokhodnyi", and was also used in the title.]

[5]There are, of course, none in the near-polar latitudes of the southern hemisphere.

Morphologically, the summer and autumn keta differ, as far as known, only in their size; the summer form is considerably smaller. According to V. K. Soldatov's (1912) data, the mean length of the male summer keta from the lower Amur is 61 cm, while male autumn keta average 65 cm (these data refer to 1907 and 1908). The number of eggs in summer keta is correspondingly smaller: 2500, as compared with 3900 among autumn keta.

Similarly, there are no morphological differences between vernal grains and hiemal grains; but hiemal grains are more hardy and have more productive growth.

The differences which distinguish autumn keta from summer keta can be summarized as follows:

1. they enter the river later than the summer keta
2. at time of entering they have less developed sexual products
3. they spawn later
4. they migrate farther upriver
5. they are larger and heavier than the summer keta
6. they are more fecund.

In abundance, autumn keta in the Amur now considerably exceed the summer keta; but before the war [World War I] it was otherwise: the summer keta exceeded the autumn.

The opinion has been expressed that the summer keta are nothing more than autumn keta younger in age. But this is not true: the summer keta in the Amur are of the same age, 3–6 years, as the autumn keta, and they also return from the sea at an [average] age of almost 4 years as a rule. Hence there is no basis for regarding them as a different age-group from the autumn keta.

The question now arises, could not a summer keta under existing natural conditions transform itself into autumn keta, or vice versa? Here we must answer no—this is impossible; for every keta, whether of the summer or the autumn run, dies immediately after spawning. In general, all Pacific salmon of the genus *Oncorhynchus* lay eggs only once in their life and perish after spawning.

[page 713] Finally, is it possible that under natural conditions we could obtain autumn keta from eggs laid by summer keta, and vice versa? Although no experiments have been conducted with keta, yet on the basis of what we know about another species of *Oncorhynchus*, the chinook salmon (*O. tshawytscha*), we must suppose that under natural conditions the eggs of summer keta must develop into summer keta, and autumn keta must produce autumn keta.

I will say a few words about the remarkable observations made by the American ichthyologists Rich and Holmes on chinook salmon migrating into the Columbia River. The native chinooks there are divided into two races—the summer chinooks, which enter the river from July to September and which correspond to the summer keta, and the spring chinooks which correspond to the autumn

keta[6]. The authors mentioned, by wholesale marking of fingerlings, showed that from fingerlings of spring races of chinooks spring spawners were obtained, and from the fingerlings of summer races they obtained summer spawners. They performed their experiments like this: eggs were taken from the Willamette River, a tributary of the Columbia where only spring chinooks spawn, and placed them in the tributaries of the Columbia where nothing but summer chinooks spawn; they hatched the eggs there and liberated them. Nevertheless, when adult, they returned from the sea as spring fish. Experiments were also made with summer chinooks: their eggs were reared under the conditions of spring fish, but nevertheless they produced summer chinooks.

In a word, it was not possible either to change the summer form to the spring, or the spring form to the summer (at least under the conditions of these experiments).

Taking all the above into consideration, I have separated the autumn keta as a special race, the infraspecies *biennis* Berg (1932, p. 115)[7] (the summer keta being the typical form). We must bear in mind that the summer and autumn keta lay their eggs in different places and at different times, and therefore the chance of forming hybrids between them is not great.

In addition to keta and chinooks, seasonal races are known for a third Pacific salmon, the sockeye (see Berg, 1932, p. 126). It is possible that they exist among other species of *Oncorhynchus* also.

Such is the situation among Pacific salmon of the genus *Oncorhynchus*. The general picture of the existence of two races appears here to be quite simple and completely definite, although the actual condition under which these races arise is not clear to us as yet.

Analogous races exist in the so-called Atlantic salmon[8] (genus *Salmo*), but here the picture is much more complex and confused. [page 714] The picture is comparatively simple for the salmon [losos] of our northern rivers, or semga[9] (*Salmo salar*, and in the White Sea *Salmo salar breviceps*). Among the semga two forms are distinguishable, a summer and an autumn form.

1. the *summer* form enters the rivers in summer with well-developed sexual products and *lays its eggs the same autumn*, without migrating very far upstream; its size is usually not very large;

2. the *autumn* form (infraspecies *biennis* Berg, 1912, p. 137) enters the rivers in autumn with weakly developed sexual products, usually migrates far upriver and *lays its eggs in the autumn of the following year*, after having spent a whole year in the river (without feeding all the while); its size is large, as a rule.

[6][This identification of the *spring* chinooks with the *autumn* keta seems rather remarkable, but it is not discussed further. Actually, what Berg calls summer chinook (letniaia chavycha) are commonly called fall chinook on the Columbia; the usual division between the spring and fall runs is made at August 1, and the fall fish continue to run into October.]

[7]See Ryby presnykh vod SSSR, 3rd Ed., Vol. I, 1932, page 15, for what constitutes an "infraspecies".

[8]To call these salmon *Atlantic* is not wholly correct, since representatives of the genus *Salmo* also occur in the Pacific Ocean.

[9][Apparently *semga* is a name applied to *S. salar* in north Russia, being more specific than *losos*, which latter can refer to salmon in general as well as to *salar* specifically. I have translated *losos* as "salmon", but retain *semga* wherever it occurs.]

The analogy with the summer and autumn keta is remarkable. But there are also very important differences. Although the autumn keta lays its eggs later than the summer keta, it does lay them in the same year. However the autumn semga delays its spawning until a year after the summer semga; in every case it winters over in the rivers, without spawning, and lays its eggs the following autumn. Hence the autumn race of semga can with complete accuracy be called, as I have done, a *hiemal* race (*biennis*), in contrast to the summer semga which matures in the same year and is a *vernal* race.

The question arises, does an autumn semga never change into a summer semga under natural conditions? V.R. Aleev (1928) thought that he had succeeded in demonstrating the transformation of a White Sea summer semga into an autumn one. Here is how the experiment was arranged. In the first half of the summer of 1924, on the Zimniaia Zolotsa River which flows into the White Sea north of Arkhangelsk, semga-"zakroika" were put into a rearing enclosure. Eggs were obtained from one semga 59 cm long and 1.48 kg in weight, and then she was marked and released. A year later, on October 11, this fish was again taken in the same river; she had only just come from the sea, and had all the external features of an autumn semga, "was clean, fat and silvery"; at a length of 67 cm she weighed 3.15 kg. So Aleev concludes that the "spring" semga of 1924 had changed into the "autumn" semga of 1925.

However, this experiment is not pertinent, for a *zakroika* is itself an autumn semga—one which has spent the winter just off the mouth of a river or just in the mouth, and in the spring (at the beginning of summer) has ascended the river.

The *grilse* of the English, or *tinda* of our northern fishermen, are salmon which have spent one winter in the sea and have ascended the river—usually in July —for spawning. Thus the tinda is a vernal form. Calderwood, an excellent observer of the biology of Scottish salmon, categorically denies any possibility of a grilse transforming itself into what I call a hiemal race and what in Britain is called a *spring salmon*—vesennii losos (1930, p. 40): "spring salmon" also have a stage analogous to grilse, but it is spent in the sea; in Scottish rivers in autumn it is possible [page 715] to observe both occasional specimens of grilse (that is, grilse of the hiemal race) and a few "spring salmon" which are their equals in age but are of even smaller size than grilse[10]. Consequently it cannot be considered that in nature [ordinary summer] grilse develop later into hiemal semga. "Spring fish cannot be bred from grilse", says Calderwood (p. 43).

Thus we have as yet no basis for believing that, under natural conditions, salmon which first lay their eggs as summer fish can next time enter the river as autumn fish.

The reverse also has never been demonstrated: that autumn salmon can make their second entry into a river as spring salmon.

On the other hand, we have no basis for insisting on a hereditary basis for the summer and autumn races in salmon. The constancy of these races might be

[10]This has also been observed in our country, on the Kola peninsula. For example, in the Ponoe River in the fall, along with the comparatively large autumn (hiemal) semga there can also be found autumn semga less than 40 cm long.

explained merely by the fact that they always lay their eggs in different places in the river, and so do not produce hybrids between the two. But it is only that this has not yet been demonstrated; it is unlikely that hybridization is *impossible*.

Even if the summer and autumn forms of salmon do not change from one to the other in the adult condition, that does not exclude the possibility that, from a single batch of fertilized eggs, we might get both the slow-growing grilse, and the faster-growing autumn salmon. For an analogy we might look to the very interesting data obtained by P. V. Tiurin (1933) concerning perch (*Perca fluviatilis*) of Lake Chana in western Siberia. In this lake there are two forms of perch:

1. morpha *phragmiteti* Berg 1933, small, slow-growing and early-maturing, lives in the emergent vegetation shoreward and belongs to the so-called "peaceful" [non-piscivorous] fishes; and

2. large, fast-growing, maturing a year later; it lives in the open part of the lake and feeds on fishes (I consider this perch to be of the typical form).

At early ages both forms live together. According to Tiurin's observations, the large perch are for the most part (83%) females. He explains this on the basis that the large perch arise from the small ones by a transformation of the part of the latter which have a carnivorous manner of life.

In a similar manner, in salmon too the fast-growing individuals might become the autumn salmon, and the slow-growing ones the summer salmon.

But among salmon the matter is very complex. Here it is impossible to make any general rule that autumn salmon are always larger than summer salmon. For example, among the salmon of the Soiana River (a tributary of the Kuloe flowing into the Gulf of Mezensk), [page 716] according to E. S. Kuchino's studies we do not find any difference in rate of growth between the summer and the autumn form:

		River period				Sea period	
Number of complete years		1	2	3	4	1	2
Summer	♂ (237 pieces)	39	89	131	162	380	682 mm
	♀ (140 ")	42	95	135	162	360	618 "
Autumn	♂ (105 ")	39	87	129	160	375	622 "
	♀ (351 ")	42	92	134	160	377	603 "

Against the possibility of any transformation of the summer semga into autumn semga we can also cite the analogy of the races of chinook salmon (*Oncorhynchus tschawytscha*) mentioned above (p. 518).

On the other hand, in our northern rivers the grilse are almost exclusively males. For example, the Niva River flowing into the White Sea near Kandalaksha, and the Teriberka, produce only male grilse; on the Soiana in 1932 there were only 9 females among 153 grilse; in collections made from the Voronia River (Murman) in 1933 there were 312 male grilse and only 9 females. In France also, grilse are observed to be almost wholly males. In Norway there are 19% females

among grilse, in the Rhine 17% and in Scotland about 50%. Among summer salmon, in general, males predominate. Among autumn salmon, by contrast, females predominate. Thus in the Niva or Voronia male grilse must as a rule spawn with female summer salmon. But it may perhaps be that they also fertilize the eggs of the autumn salmon?

Special experiments are needed to decide these questions.

Such are the semga of the Murman, the White Sea and the Pechora.

But in the Atlantic Ocean the state of affairs seems more complex. In the Rhine, along the coasts of France, in England and in Scotland the summer (vernal) salmon behave much the same as in our north, but the hiemal salmon are for the most part not autumn fish but winter fish: their principal migration takes place from December or January and continues into March (although the run begins in the autumn). In a word, in the warm climate of the Atlantic littoral we observe an analogy with the hiemal cereal grains of our southern regions—the pre-Caucasus and Turkestan, where these grains are sometimes sown in January.

Let us consider in more detail the biology of the Scottish salmon. Small autumn salmon with poorly developed sexual products (called *spring salmon* in English) begin to enter Scottish rivers from the ocean as early as the second half of September. These salmon will lay their eggs the following year in October or November. But the main run of this race, which reaches a size of 15 kg, belongs to February, March and the beginning of April. Toward the end of May the "spring salmon" usually cease to be caught at the mouths of the Scottish rivers. But here is what is remarkable. In April and May, along with the "spring" salmon, summer salmon begin to appear [page 717] in the river. In size, form, colour, and condition of the eggs and milt they cannot be distinguished from the spring salmon, and the fishermen do not distinguish them. They can be distinguished only by the scales, on which are imprinted the history of their feeding conditions: the summer salmon have fed immediately before entering the river, while the spring salmon had ceased to feed some considerable time previously, during the cold part of the year, and during the following months exhibit little growth (Menzies, 1931, pp. 109–110).

Thus, although in principle the difference between the hiemal and the vernal race is preserved, in details the situation seems much more complicated than among the salmon of our northern rivers.

Both with us and in Scotland, among both the autumn and summer salmon running into the river from the sea, there are individuals which have spent one winter in the sea, two winters, three winters and occasionally even more[11]. Why does one salmon come into a river to spawn after spending only one winter in the sea, when for another a similar instinct brings it back after two years, and a third, after three? Some suggest that even these kinds of salmon represent separate forms or races, each of which is distinguished by its own special length of sojourn in the sea before first spawning. But, as Menzies says (p. 198), is it really possible that these "races" do not mingle on the spawning grounds, where the eggs of a

[11]In Scotland examples are known, rare to be sure, of salmon that have spent 5 successive years in the sea (Menzies, p. 97).

salmon of one group may be fertilized by the milt of a salmon of another group, a year or two older or younger? Specially designed experiments are required to decide this question.

In general, there is still much that is puzzling in the biology of salmon, even though much work has already been done on these fish, both here and abroad.

This same existence of two races is observed in another fish related to the salmon, the kumzha[12] (*Salmo trutta*), although here the phenomenon seems more complex for the kumzha has the habit of entering rivers on non-spawning [as well as spawning] migrations; such kumzha, having spent some time in the river, return again to the sea. In Scotland a large part of the kumzha lay their eggs in the same year as they enter the river (Nall, 1930, p. 253); but in the River Tweed, for example, part of those entering in early winter lay their eggs during that season, but a larger part will not spawn until the following winter (Nall, pp. 173, 255). Fish which enter during spring and summer lay their eggs the same year. Thus here too a vernal and a hiemal race occur. The existence of these two races is indicated also for the kumzha of the Rhein. The same has been shown for the kumzha of the Ponoe River (Kola Peninsula) from the observations of the Institute for Lake and River Fisheries in 1932 (A. G. Smirnov).

Vernal and hiemal races are especially clearly developed in the Caspian salmon [losos] *Salmo trutta caspius*. This salmon is close to the kumzha (*S. trutta*) in number of scales, but in number of gill rakers it approaches the northern salmon (*S. salar*). I assign it to *S. trutta* on the basis of the fact that in rivers of the Caspian basin [page 718] it develops a freshwater form that never migrates to sea —the trout [forel] *S. trutta caspius* morpha *fario*. And a capacity to develop trout forms is one of the characteristic features of the kumzha. However, the possibility is not excluded that the Caspian salmon is an offshoot of the northern salmon, *Salmo salar*, which in the Caspian has changed some of its features in the direction of the kumzha.

However that may be, among the Caspian salmon there are two races.

1. *Vernal*. This race enters the Kura River in October with almost ripe sexual products; its weight is comparatively small—not over 12 kg; and it does not go very far upriver—not over 600–700 km from the mouth (i.e., no higher than the middle reaches of the Kura) and spawns the same year. The numbers of the vernal salmon or *lokh*, as they are called on the Kura, are insignificant in comparison with the hiemal race: in the autumn of 1915 in the lower course of the Kura at the Bankov fishery 49 female and 13 male "lokh" were taken, while more than 20,000 of the hiemal race were taken.

2. *Hiemal*. This race begins to enter the Kura in October, but the main run arrives in November and December. The hiemal race, having poorly-developed sexual products, goes very far up the Kura—above Tiflis to Akhaltsikh and the confluence of the Aragva, and spawns in the uppermost parts of the rivers in October–November, about 9–11 months after entering the Kura from the sea.

[12][Here again I will use the Russian word in the English text to avoid possible confusion. The nearest English equivalent of kumzha is "sea trout" but, in America at least, this term usually refers to a general rather than a specific category of salmonids.]

This race is much larger than the summer race, reaching 51 kg (so large an Atlantic salmon has never been reported, but that doesn't mean that these fish necessarily are kumzha on that account)[13].

Since both races enter the Kura almost concurrently and since the vernal Caspian salmon are caught only by tens, whereas hiemal ones are caught by thousands, here the hypothesis that vernal Caspian salmon in nature transform into hiemal ones is impossible.

In the rivers of the south Caspian there are also two races, but in detail they exhibit many peculiarities; in general they are very poorly known. In the rivers of the Kubin coast of the Caspian there are apparently only small, vernal salmon ("lokh") of 2–3 kg weight.

In the rivers of Samur (Dagestan) and in the Terek both races occur. At the present time salmon enter the Volga only in small numbers, but in the 17th Century, according to A. N. Derzhavin's (1934) information, many were caught in the Volga up as far as Kazan (and apparently even farther), in the Oka, and in the Kama. From a study of 500 specimens of salmon from the Volga delta Derzhavin showed that its run lasted from August (5.8%) to December (0.2%), the peak of the run being in October when 56.5% of the total were caught, in September 17.2%, and in November 20.2%. The mean weight of this salmon is 8.7 kg (maximum 22 kg); it is a hiemal salmon. Vernal [page 719] salmon are scarcely to be found in the Volga, although the possibility that a few individuals enter is not excluded.

Among other salmonids, we observe the presence of two races in the Arctic char *Salvelinus alpinus*[14]; they may possibly occur among the Arctic omul (*Coregonus autumnalis*).

STURGEON FAMILY

Vernal and hiemal races are developed extremely clearly in acipenserids, although up to now this phenomenon has not been recognized as parallel to what has been observed among salmonids. We will present briefly the facts pertaining to this question, dwelling, because of limitations of space, mainly on the acipenserids of the Caspian Sea.

SEVRIUGA

The sevriuga or stellate sturgeon (*Acipenser stellatus*) begins to enter the Ural River from the Caspian Sea at the middle of April; the run continues through May. The spawning of this sevriuga—we must call it a vernal race—takes place in

[13]I will quote from the data of V. N. Beliaev (1932) the monthly average catches of salmon, in thousands of individuals, taken in the lower Kura during the years 1922/23 to 1927/28:

X	XI	XII	I	II	III	IV	V	Year
0.8	6.8	9.5	3.1	1.6	0.4	0.1	0.02	22.3

[14]Observations of A. N. Probatov in the Kara River flowing into the Gulf of Kara (see Berg, 1933, p. 842).

May and June. The main period of fishing for these fish occurs in the Ural during the months mentioned.

But from the middle of August sevriuga again begin to enter the Ural and continue to do so up to the middle of October; this sevriuga lies over winter in the river in deep holes[15] ("yatovi")[16], and in spring it ascends and lays its eggs in May. These evidently are *hiemal* sevriuga; they are considerably smaller than the vernal ones.

In his remarkable writings concerning the life of the sturgeons of the Ural River, N. Severtsov (1863) has pictured the life of the sevriuga in that river in the following manner; in spring it enters from the sea into the lower reaches of the Ural and lays its eggs, then it returns downstream to the sea; at the beginning of autumn it again enters the Ural, and winters there in the yatovi; in spring it goes farther upstream, lays its eggs, and again returns to the sea. Thus on this basis there is only one race of sevriuga, which lays its eggs every year, spending the winter alternately in the river and in the sea. But in my opinion this picture is wrong: we have two races of sevriuga, one the vernal race, the other hiemal. It is difficult to imagine that a sevriuga which has laid its eggs in May or June could succeed in returning to the sea, mend itself there and build up enough food reserve to be in condition to go upriver again at the middle of August. (In the river the sevriuga apparently feeds very little; see Derzhavin, 1922, p. 87.) For the Don sevriuga, which in its general mode of life is similar to the Ural, this is impossible—simply because of the times involved: it spawns from the second half of May to the end of June, and the summer–fall run begins there as early as June.

[page 720] In the Volga the sevriuga behaves similarly to what we know for the Ural. I will cite the very valuable data concerning the catches of sevriuga in the north Caspian, reported by Grimm (1893). They pertain mainly to the region off the mouths of the Volga and to the delta of this river and they represent the landings of one important fishery in the Volga delta. The figures are the mean monthly catches in number of fish for the years 1879–1892 old style[17]:

	Pieces	%		Pieces	%
Jan	3	0.01	July	356	1.8
Feb	–	–	Aug	602	3.1
Mar	272	1.4	Sept	442	2.3
Apr	6457	32.9	Oct	236	1.2
May	6908	35.2	Nov	23	0.1
June	4308	22.0	Dec	6	0.03

[15][Yamy (singular, *yama*), literally pits; here, depressions in the bed of the river, for which the best colloquial English is "hole" or "deep hole"—as in "the old swimming hole".]

[16]The word *yatov* comes from the Turkish root *yat*—to lie. Literally translated, a yatov is a zalezhka or lezhbishche.

[17][This refers to the Julian calendar, which was used in Russia up to 1918. At that time it was 13 days behind the Gregorian calendar ("new style"); that is, January 1 old style= January 14 new style.]

As we see, the principal run of sevriuga from the Caspian into the Volga occurs in spring; the sevriuga begin to ascend the river with the disappearance of the ice, and large numbers are observed from the middle of April to the end of May. This—vernal—sevriuga for the most part lays its eggs the same season, in May, June and partly in July in the lower and middle Volga, from Akhtuba to Tetiush (Berg, 1911, p. 302). However, as early as June sevriuga begin to be encountered, in the lower Volga, which have poorly developed eggs and sperm—apparently individuals of the hiemal race. Hiemal sevriuga continue to occur up to November, but their run is very light compared to the vernal run, as the above tabulation shows. Occasional individuals lie in the lower reaches of the Volga over winter, in the deep holes or "yatovi". In spring and at the beginning of summer of the following year the hiemal sevriuga, which have wintered over in the river, will lay their eggs. According to the observation of A. V. Podlesny (1930), in the lower Volga between Vladimirovskaia and Dubovkaia these sevriuga spawn in two groups:

1. in flood channels [v poloiakh], from the end of May to July at a depth of 1½ to 2 m;

2. in the main Volga, in mid-channel, from the middle of June to August, at depths of 9 to 13 m.

In all probability the hiemal sevriuga spawn early in the flood channels, and the vernal sevriuga spawn later in the main Volga. We must suppose that the vernal sevriuga spawn in the lower part of the Volga and the hiemal sevriuga farther upstream. All these suppositions require verification, but they are based on information which is true of the Kura sevriuga.

In the Kura the sevriuga also ascend twice—in spring and in autumn. The autumn run, although much less important than the spring run, is nevertheless much better developed than it is on the Volga: in the lower reaches of the Kura at the present time not less than 10% of the yearly landings of sevriuga are taken in October (while 40% are taken in May). In the first half of the 19th century the autumn run of sevriuga in the Kura was even more important than at present (although still considerably less than the spring run) as is apparent from the [page 721] averages shown below, which are computed from the data of Ber and Danilevsky (1863) extending over 26 years (1829–1845 and 1847–1855), old style, and pertaining to the lower reaches of the Kura (the great Bozhii fishery):

	Jan	Feb	Mar	Apr	May	June	
Pieces	613	898	26240	52030	18590	5471	
%	0.3	0.2	16.1	31.9	11.4	3.2	
	July	Aug	Sept	Oct	Nov	Dec	Year's total
Pieces	1288	3644	21613	26468	7551	330	156614
%	0.5	2.0	13.3	16.3	4.6	0.2	100

Concerning the Kura sevriuga, A. N. Derzhavin (1922, p. 105) writes: "at the time that some autumn females possess developed ovaries and have become ready to lay their eggs during the current spawning season, other individuals have a relatively low index of ripeness; there is no doubt that their small eggs could achieve maturity only in the following season". At Mingechaur (middle course of the Kura), where the principal spawning grounds of the Kura sevriuga are situated, in August sevriuga can be seen in two stages of maturity: some will lay their eggs within a very short time, others only in the next year; in late autumn at this place the only sevriuga encountered are those which lay their eggs the following spring (Derzhavin, p. 106).

The spawning period of the sevriuga on the Kura extends from the middle of April through the middle of September, and for a few individuals even to the middle of October, new style (Derzhavin, p. 163).

I postulate that the Kura vernal sevriuga spawn in summer, and the hiemal ones in spring. Pertinent to this suggestion are certain observations of A. N. Derzhavin, according to whose data (p. 163) the sevriuga which winter in the Kura spawn in the spring; their spawning does not last very long, up to the middle of May, because, Derzhavin says, an intensive fishery in the lower course of the Kura prevents the arrival of new spawners. But I do not believe the cause lies there; rather it lies in the peculiarities of the biology of the hiemal sevriuga. The vernal sevriuga begin to lay their eggs a month after the hiemal, at the middle of June; at Mingechaur their principal spawning is in July. In a similar manner vernal grains mature later than hiemal ones.

Thus the main part of the sevriuga in the Ural, the Volga and the Kura belong to the vernal race.

Osëtr

The biology of the osëtr or Russian sturgeon (*Acipenser güldenstädti*) is more complex. At first glance it might be assumed that the Volga osëtr has only a single hiemal race. But in fact the spawning of this fish takes place in the middle Volga in May, whereas the run into the Volga delta from the Caspian begins later than the run of sevriuga, at the beginning of June. Thus the osëtr running in May will lay their eggs only in the following year [page 722] after having wintered in the river. This is well known on the middle Volga; there, in the reaches between Kamyshin and Saratov the main run of osëtr is in the first half of the summer, while spawning takes place there beginning in the first days of May; obviously the spawning osëtr are those which arrive there the previous year. Thus in the Volga there are hiemal osëtr, without any doubt.

However, the data collected by A. N. Derzhavin (1913, p. 15) show that the first approach of osëtr to the Volga delta (Olia village) was recorded at the observation point of the Astrakhan Ichthyological Station as early as March 23, new style; since observations were not made during the winter, by analogy with the Kura (for which see below), we can postulate with considerable assurance that the first arrivals show up at the beginning of March.

The above is supported by Grimm's (1893) data concerning the catches of osëtr in the Volga delta and off its mouths. Mean monthly number of pieces of osëtr for 1879–1892, old style, were as follows:

	Pieces	%		Pieces	%
Jan	13	0.1	July	2136	12.7
Feb	12	0.1	Aug	1024	6.0
Mar	324	1.9	Sept	515	3.0
Apr	4123	24.5	Oct	246	1.5
May	4829	28.7	Nov	77	0.5
June	3518	20.9	Dec	19	0.1

Because, according to the observations of A. V. Podlesny (1930), it appears that osëtr lay their eggs in the lower reaches of the Volga beginning at Vladimirovka (near Yenotaevsk), evidently the vernal osëtr which enter the Volga in the early spring have sufficient time to proceed to their spawning grounds during the same year.

Grimm (1896, p. 80) has already noticed that in the Volga delta "osëtr of the winter run, up to March, all go [directly] to the spawning grounds, but those of the summer run go farther upstream and spawn in the spring of the following year". Consequently among the Volga osëtr, as among its sevriuga, there are two races—hiemal and vernal; but among the osëtr, in contrast to the sevriuga, *the hiemal race predominates.*

The above is confirmed by the biology of the osëtr on the Ural River. According to the observations of N. Severtsov (1863), osëtr begin to go up the Ural from the Caspian in the middle of April, new style, right after the beluga and sharpnose sturgeon, and almost concurrently with the sevriuga or slightly earlier than it. These evidently are vernal osëtr. In the delta of the Ural and Gurev, spawning of osëtr is observed in the *middle of May.* This, we must suppose, is the spawning of the vernal osëtr. A more intensive run of osëtr in the Ural begins at the end of May; and it continues up to the end of the summer, although tapering off. These, hiemal, osëtr lie throughout the winter in holes in the bed of the Ural River between the village of Kalenovsk (which lies between Gurev and Uralsk) and Uralsk. In spring they go higher and lay [page 723] their eggs in the region of Uralsk *at the end of April or beginning of May.* Thus the hiemal osëtr go farther upriver and, like the hiemal sevriuga, lay their eggs earlier than the vernal race.

In the Ural River the hiemal race of osëtr predominates, as it does in the Volga.

The situation is different on the Kura River. According to Ber and Danilevsky's (1863) data the run of osëtr in the lower Kura (the great Bozhii fishery) for 1829–1855 was distributed on the average in the following manner (old style):

	Jan	Feb	Mar	Apr	May	June	
Pieces	44	302	3864	4536	1290	1101	
%	0.1	1.4	23.2	27.1	7.7	6.3	
	July	Aug	Sept	Oct	Nov	Dec	Year's total
Pieces	694	1366	1733	1801	505	58	16154
%	2.8	7.2	10.3	10.8	2.9	0.2	100

Here the main run of osëtr takes place in the second half of April, new style, and the main spawning is *at the end of July and in August*. However, according to V. N. Beliaev's (1933, p. 72) observations, the part of the osëtr which enter the Kura at the end of May and in the summer and autumn months have sexual products in stage III, that is, far from being mature[18]; these osëtr winter over in the Kura and lay their eggs in the following year, and "a spawning, apparently of this group of osëtr, occurs *in the second half of April and in May*". Thus the Kura hiemal osëtr, just like the Kura hiemal sevriuga and the Ural hiemal osëtr, lay their eggs earlier than the vernal osëtr.

Consequently, comparison of the biology of the Kura and the Volga-Ural osëtr shows us that in the north Caspian hiemal osëtr predominate and in the south Caspian vernal osëtr do. Also, according to V. N. Beliaev's information, the southern osëtr can be separated biometrically into a special form, the subspecies *Acipenser güldenstädti persicus* Borodin (see Berg, 1933, p. 836).

On the Dnepr River also the vernal osëtr predominate over the hiemal.

Beluga

A completely analogous picture is presented by the beluga or great sturgeon (*Huso huso*). In the Ural River the vernal beluga begins to arrive starting in the middle of March; this beluga lays its eggs in the delta of the Ural at the middle of May. The beluga which enter the Ural toward the end of the spring and early summer, and also in the autumn, belong to the hiemal race; this race lies all winter in the river, in the yatovi, then in spring it goes up the Ural to lay its eggs at the beginning of May. Hiemal beluga predominate, by numbers, in the Volga delta, where the main part of their run is in September to November.

[page 724] In the north Caspian immediately off the mouths of the Volga and in its delta, the mean monthly catches of beluga, averaged over the years 1879–1892, old style, were as follows according to Grimm (1893) (in pieces):

[18]Sexual products completely ready for fertilization are designated as stage V.

	Pieces	%		Pieces	%
Jan	85	1.2	July	283	3.9
Feb	158	2.2	Aug	919	12.7
Mar	834	11.5	Sept	1577	21.8
Apr	554	7.7	Oct	1227	16.9
May	317	4.4	Nov	732	10.1
June	334	4.6	Dec	217	3.0
			Year's total	7239	100

In the Kura, where beluga to-day are caught only occasionally, those most frequently encountered are vernal beluga, according to information of the Azerbaijan Station; however 75–100 years ago the hiemal race predominated, as in the mouths of the Volga. This is indicated by the excellent statistics of the Kura fishery collected at that time by Ber and Danilevsky, which we have already cited. In the lower reaches of the Kura in the great Bozhii fishery, for the years 1829–1845 and 1847–1855, the mean catches of beluga were as follows, old style:

	Jan	Feb	Mar	Apr	May	June	
Pieces	64	71	129	23	3	0.5	
%	4.7	5.4	12.4	2.2	0.3	0.1	
	July	Aug	Sept	Oct	Nov	Dec	Year's total
Pieces	0.7	32	146	297	220	105	1004
%	0.1	2.0	14.0	28.6	21.0	9.0	100

Sharpnose Sturgeon [Ship]

Sharpnose sturgeon (*Acipenser nudiventris*) enter the Kura River twice, in spring and in autumn. The spring run reaches its maximum in March and the autumn run in October to November, new style. From Ber and Danilevsky (1863) we will cite the following data relative to the catches of sharpnose sturgeon in the lower reaches of the Kura (in the great Bozhii fishery) for the years 1841–1855, old style:

	Jan	Feb	Mar	Apr	May	June	
Pieces	251	988	3578	847	116	26	
%	2.0	8.1	31.6	7.5	1.0	0.1	
	July	Aug	Sept	Oct	Nov	Dec	Year's total
Pieces	11	86	1098	2776	1744	244	10502
%	0.02	0.4	9.0	22.7	15.4	2.2	100

Since the spawning of the sharpnose sturgeon takes place in the Kura at the end of April and in May it is obvious that here too there are two races, as among the other sturgeons. The vernal race of sharpnose sturgeon predominates in the Kura. However, in the basin of the Aral Sea only the hiemal sharpnose is found (Berg, 1911).

[page 725] Thus in all the anadromous acipenserids we have two well-developed races—vernal and hiemal, of which now one will be the more important, and now the other. Rarely one of the races can be completely lacking, as is true of the Aral sharpnose sturgeon.

Sterlet

The sterlet (*Acipenser ruthenus*) is a freshwater fish which does not go to sea. However, in the region of the Volga just off the mouths (and also in the regions of the deltas of the Don, the Dnepr and other Black Sea rivers) there are semi-anadromous sterlets which enter the Volga delta twice: in spring along with the sevriuga and then in autumn. The spring (vernal) sterlet goes higher up the delta for spawning; fish of the autumn (hiemal) race lie in the deep holes during the freeze-up—either immediately off the mouths of the Volga, in the mouths themselves, or in the lower part of the delta (V. E. Yakovlev, 1870; see Berg, 1911, p. 217). Where the hiemal semi-anadromous sterlets spawn is not known (in general, in the Volga, spawning places of the sterlet have not been found any farther downriver than Chërnyi Yar, 400 km from the mouth, but it is possible that they also occur much lower; see Chugunov, 1928, p. 101).

Concerning the freshwater sterlet in the Volga Basin there are no accurate observations regarding the existence of seasonal races, but indirect information suggests that such races may occur. For example, in the River Viatka near Malmyzh, in the spring at the time sterlets are running fishermen distinguish two groups: some begin to run immediately after the break-up of the ice, and stay close to the bank; among these sterlets the sexual products even in the largest ones are far from mature; for example, one sterlet 62 cm long taken June 8, 1929, contained eggs in stage II–III; without question this sterlet would have had to lay its eggs in the following year, 1930. This apparently is a hiemal sterlet. Other sterlets, which migrate in the spring out in mid-channel, have ripe eggs and milt; these evidently are vernal sterlets; their spawning was ovserved near Malmyzh in the main channel on May 23–28, 1930 (Lukash, 1933, pp. 31–32).

LAMPREY FAMILY

In rivers emptying into the Baltic Sea and its gulfs, particularly the Neva, the lamprey (*Lampetra fluviatilis*) has two races—an autumn and a spring one. In autumn in the Neva a mass migration of lampreys is observed entering from the Gulf of Finland; they winter in the river, then lay their eggs in the first half of June (sometimes toward the end of May). The autumn run begins in appreciable numbers in August, the main part of the run is in September, October and November; but a few individuals of the hiemal minoga begin to enter the river as

early as the first 10 days of June (Ivanova-Berg, 1932). In spring lampreys again approach the Neva delta, at which time they already have well developed sexual products; these lay their eggs the same season.

[page 726] Apparently here too we have a case of two races, hiemal and vernal. It is curious that in the Tiber the lamprey run is very late (similar to the Caspian salmon in the Kura): at the mouth of the river it lasts from December to April.

CARP FAMILY

It is well known that the anadromous cyprinids, for example the vobla, bream and others, approach the Volga and Ural River deltas twice–in spring and in the fall. It is my opinion (though it needs confirmation) that these approaches are associated with the presence of two races–vernal and hiemal. Let us consider the vobla.

Vobla (*Rutilus rutilus caspicus*) migrate to the Volga delta from the northern part of the Caspian Sea at two times of year: in spring, when they spawn, and in fall, when they have in view the spawning of the following year [imeia v vidu nerest v sleduiushchem godu]. Large vobla come in autumn, smaller ones in spring. The autumn run, according to Tereshchenko's data (1913, p. 7), begins in June and lasts to late autumn, reaching its maximum in October. "Not long after the break-up of the ice on the river large specimens of this fish, which wintered in the river or just off the mouths of the Volga, move out of the depressions in the river bed and proceed upstream." The main run of vobla begins about 2–3 weeks after opening of the river and lasts from the middle of April through May. The sex composition of the autumn and spring vobla is different: in autumn there are very few males, while in spring they average 47%, or in exceptional instances up to 70% (p. 16). Analogous sex ratios are known also for autumn and summer semga: among the autumn fish males predominate, among summer fish, the females. The size of autumn vobla, as I have said, is large:

	Year of hatch	Sex	Spring 1912	Autumn 1912
			mm	*mm*
3-year-olds	1909	♀	131	197
3-year-olds	1909	♂	122	179
4-year-olds	1908	♀	191	216
4-year-olds	1908	♂	160	190

The condition of the sexual products of autumn vobla is of course much less advanced than in the spring vobla.

How far upriver the spring vobla go, and how far the autumn vobla go, is not known. Apparently the spring migration of autumn vobla begins earlier, and it lays its eggs earlier, than does the spring race.

The Volga–Caspian bream (*Abramis brama*) comes to the Volga delta three times–in spring, summer and autumn. In contrast to the vobla, the greatest run of

bream occurs in autumn–in September, October and November (Tereshchenko, 1917). The biology of the bream has not been studied from the point of view which interests us here, but apparently it too has seasonal races. At least A. N. Derzhavin (1913, p. 33) pictures the run of bream to the Volga delta in 1911 as follows: Right after the under-ice [podlednaia] vobla (that is, the autumn vobla) and the sanders [*Lucioperca*] there arrive in the outer parts of the delta the deep-hole bream [yamnyi leshch] which ever since autumn have been wintering [page 727] off the mouths of the river and in the deep holes of its lower branches. Then there appear great schools of bream moving in from the sea, that is, bream of the spring race. At the Olia fishery in the Volga delta the main run of the spring bream (which had come from the sea) was on the 22nd and 23rd of April.

In the Kura River bream enter during the winter–from December to February; the peak of the run is in January (Beliaev, 1932).

The carp (*Cyprinus carpio*) behaves in a similar way in the Volga delta. It arrives at two seasons, spring and autumn. The autumn, or deep-hole carp, resemble the autumn bream, and go upstream in spring earlier than the spring or "sea" carp (Derzhavin). In other rivers also the carp appears twice–in spring and fall.

The cut-tooth [vyrezub], *Rutilus frisii* (Nordm.), approaches the Dnepr–Bug littoral twice, in spring and autumn. The spring run lasts from March to the end of April; it spawns in the Bug in the region of the rapids from the end of April through the first half of May. The *larger, autumn, run* begins at the mouth of the Bug in the second half of August (and even earlier), the main part of the run is in August and September; in the mouth of the Dnepr the run begins in October, reaches its maximum in November and lasts in both rivers to the freeze-up (second half of December). The migrating cut-tooth in the Dnepr, both in the spring and in autumn, are far from sexual maturity; both eggs and milt are in Stage II (Syrovatsky, 1929, pp. 151, 153). However in the Bug the autumn cut-tooth are in Stage III, and toward the end in Stage III–IV, while the spring run up to the middle of May are IV and IV–V, and from the middle of May onward cut-tooth are found either in Stage V or in Stage II (Syrovatsky, 1933, p. 43); that is, both vernal and hiemal fish occur at the same time. These latter will remain in the river a whole year.

In the Caspian Sea *Rutilus frisii* is represented by the sub-species *R. frisii kutum* (Kam.). In contrast to the cut-tooth, the kutum has its maximum run not in autumn but in spring, though both races occur. Average catches in the Kumbashinka River (southern part of the Caspian, in the Lenkoran region) for the years 1925–1929 were as follows, in thousands of pieces:

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Year
1.0	7.4	113.4	160.0	–	–	–	–	–	–	0.9	0.5	283.2

The spawning run reaches its maximum in the second half of March through the middle of April; spawning occurs from the end of March to the end of April.

The third form of *R. frisii* is the subspecies *meidingeri* (Heckel), which lives in lakes of the Danube basin (Lakes Traun, Atter, Mond and Chiem) and bears the names *Frauenfisch* and *Perlfisch*. It never goes to sea, spending its whole life

in the lake; only for spawning does it enter rivers during the first half of May; at other times of year it does not occur in rivers. Seasonal races have apparently not been observed.

[page 728] The Aral barbel or usach, *Barbus brachycephalus* Kessler, enters the Amu-dar mainly in June-September, with sex organs in Stage II–III of development (M. I. Markun, 1933, pp. 26, 32). This apparently is a hiemal usach, which will spawn in the Amu-dar in spring of the following year. The run of the hiemal race begins as early as May and ends in October–November. But in addition there is a much less numerous spring run; it starts in the middle of March; on May 7, 1930, at Muinak (situated on the sea near the mouth of the Amu-dar) M. I. Markun caught a usach with eggs in not less than Stage IV of maturity (p. 32); this female, which undoubtedly would have spawned the same season, belonged to the vernal race.

Apparently there is a hiemal and a vernal race of the Kura shemaia (*Chalcalburnus chalcoides*). This fish enters the Kura from the Caspian Sea from October to April; the main part of the run is in December and January (Beliaev, 1932). They go upriver very quickly, as far as Aragva, where they are observed near Ananur in April and May (old style). The spawning is in spring, but just where and when is not known for the Kura (in the Tereka it is about the middle of May).

The chekhon (*Pelecus cultratus*) also has seasonal races: in the Don it ascends from the Gulf of Taganrog twice: in spring there is a small run to the spawning grounds (spawning is from the first days of May to the middle of June); the summer–autumn run, a much larger one, begins in July and lasts about to freezeup (V. N. Tikhonov, 1928).

Very remarkable are the races of the Issyk-kul osman, *Diptychus dybowskii*. This fish, one of the carp family native to the waters of central Asia, imitates to an amazing degree the salmonid fishes which are lacking where *D. dybowskii* lives. In the spawning period the dorsal fin of the male osman elongates, somewhat in the manner of the same phenomenon in grayling. Eggs of the osman are large, as in salmonids; they number 5000 to 25,000, and develop slowly. And the way of life of these fish recalls what exists in salmonids. There are two races of osman, a summer and a winter one: the summer osman are smaller, they are caught in summer, they spawn in the second half of June and July, for which event they enter the lower reaches of rivers. The winter osman are larger, they are caught in winter and spring: according to information obtained by our 1930 Expedition (M. I. Fedorova) it spawned in that year in the first half of April; according to the fishermen spawning takes place in the lake itself, alongshore, and begins as early as February.

PERCH FAMILY

The sander (*Lucioperca lucioperca*) which enter the rivers of the Black, Azov, Caspian and Aral Seas also have two runs–in spring and in autumn, associated apparently with the existence of two races, vernal and hiemal. In the Volga delta the "deep-hole" (i.e., autumn) sanders move upstream in spring earlier than the spring (vernal) sanders, as is true also of the deep-hole vobla, bream and carp.

[page 729] According to V. V. Petrov's (1934) information, the autumn run of sanders in the Ural River begins at the end of July or beginning of August; its peak is in the second half of October, and by the end of November, with the beginning of the freeze-up, the run stops. The spawning places of the hiemal sanders are far up the river, none below Uralsk. The spring run, much less important, begins right after the opening of the Ural; in 1931 the main spring run in the delta ended about May 1, but odd fish were taken up to the beginning of June; in all likelihood this, vernal, run ascends only to the region of Redut or Yamanka.

CONCLUSIONS

Thus vernal and hiemal races, in the very varied groups of fish which we have reviewed, have a number of common features:

1. The hiemal races spend the coldest time of year either in the river itself or immediately off the mouth of a river, while the vernal races enter the river at higher water temperatures.

2. Throughout the very cold time of year the hiemal races are in a state of vegetative quiet, when they eat little or nothing at all; many lie during the winter in deep holes in the river bed; in vernal races the stage of vegetative quiet, if there is one, is much shorter, and hibernation in depressions does not occur.

3. The vernal races lay their eggs during the same growing season as they approached the river mouth; the hiemal races do it either in the following season or at least after a considerable interval of time.

4. The hiemal races usually spawn earlier than vernal races (that is, they mature, in a given year, earlier than the vernal fish).

5. Hiemal races commonly go farther upriver than vernal.

6. Fish of hiemal races are usually larger than vernal fish.

7. Hiemal races are usually more fecund than vernal.

The analogy with vernal and hiemal races of cereal grains is remarkable. Hiemal grains also must be subjected to cold for a longer period of vegetative quiet than must vernal grains; they mature earlier, produce heavier kernels and have a higher vegetative growth than vernal varieties.

Turning to what might cause the phenomenon of vernal and hiemal races in fishes, I must say that nothing is known on this subject, for the question of the existence of such races, on the scale indicated in this paper, has not been raised heretofore in the literature.

But it is possible to make some suggestions, based on the analogy with vernal and hiemal grains. Hiemal types of grains are those which, when sown in spring, do not form heads during that same growing season. Their sprouting seeds or young plants require the action [page 730] of low temperature on them for a certain length of time; only when they have first been subjected to the influence of cold can they produce heads. By contrast, the vernal grains, when sown in spring, produce heads the same summer[19].

[19]However, almost all vernal wheats can also be sown in autumn and will then produce heads if they aren't killed by freezing.

In a similar manner the hiemal races of fish also require, for maturing their eggs or milt, a stay in more or less cold river water for several months.

The differences between vernal and hiemal races in fish has great importance for the fishing industry, and especially for fish culture. As an example I will cite our northern salmon, or semga. There, as a rule, the hiemal salmon are generally found to be larger and therefore more valuable than the vernal. But they cannot be caught with mature sexual products in the lower courses of rivers, and therefore it is necessary either to obtain spawners in the upper tributaries, which is very difficult and frequently impossible, or else retain them in holding ponds in the lower part of the river, which is also difficult when it lasts for any long period of time.

Therefore the possibility of changing a hiemal race of fish into a vernal one would have great practical interest. As we have seen, in nature the transformation of one race into the other does not occur; at least no undoubted evidence of such transformation has been produced. But *we must suppose that experimentally such a transformation could be successful.* The analogy with the vernal and hiemal grains gives this hope. "All the hiemal kinds of grains are not hiemal to the same degree, and the vernal kinds do not all have the same degree of 'vernality'," says Lysenko (1932, p. 10). Some vernal wheats, which when sown in spring produce heads the same summer at Odessa and Kharkov, will not produce heads when sown in the north Caucasus—that is, they behave like hiemal varieties. On the other hand, if we hold sprouted seed of a hiemal wheat in the cold for a while, that wheat behaves like a vernal wheat (Lysenko, 1932). Cases are known where hiemal wheat, on being sown *very early* in spring, have produced heads the same summer; but they of course are subjected to cold for a considerable time, so that in reality they are still hiemal wheat.

In general it seems unlikely that the differences between vernal and hiemal races of anadromous fishes are anything that would be firmly fixed, judging by general experience. Even the matter of whether a given species or form is migratory or sedentary is a character readily susceptible to change. For example, the carp of the Volga delta is an anadromous or, more accurately, a semi-anadromous fish (it does not as a rule go out into salt water, remaining in the brackish parts off the mouths of the Volga); but above the delta there live non-anadromous carp, which do not take part in the migration to the pro-estuarine area, and which apparently do not have [page 731] seasonal races. *Barbus brachycephalus* in the Aral Sea is a typical anadromous fish, but in the River Chu, which in respect to its fauna belongs to the basin of the Aral Sea but does not now flow as far as the Syr-dar, the local usach has a non-migratory mode of life. The salmon, *Salmo salar* — a typically anadromous fish — develops forms in the lakes of northern Europe (Ladoga, Onega, Vaner, etc.) which never go to sea and which complete their migrations within the confines of the lake system: for spawning these salmon move out of the lake into rivers tributary to it, and then return to the lake. And in southern Norway a dwarf salmon has been described which is able to spawn in the lake itself, without ascending a river. What is more, the salmon, *Salmo salar,* can spawn even in ponds, as has been observed in England and

recently in Denmark, without ever having been in the ocean or even in a large lake[20]. Finally, male salmon (but not females) can become sexually mature before going to sea, and in rivers sexually mature milt-producing males 10–20 cm long are encountered. The anadromous kumzha (*Salmo trutta*) gives rise in rivers to a non-migratory, purely freshwater form, the trout (*Salmo trutta*, m. *fario*). The same is known for some Pacific Ocean fishes, the dolly varden char (*Salvelinus malma*), the sockeye (*Oncorhynchus nerka*) and others. The anadromous lamprey, *Lampetra fluviatilus*, gives rise to the brook lamprey, *L. planeri*, which never goes to salt water.

In a word, fishes are very plastic in their biological relationships with respect to whether they are anadromous or not. But seasonal races have been differentiated, we must suppose, after the fish became anadromous (this hypothesis requires verification!)[21], and therefore it is a wholly natural assumption that vernal and hiemal races, in fishes as in grain, should not be unchangeable[22].

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[20]I called attention to this in "Priroda", 1933, No. 2, p. 69.

[21]It is possible that there are seasonal races even among non-anadromous, purely freshwater fishes. At least many river fishes, for example the sterlet and others, go upstream to spawn in spring.

[22]Concerning the alteration of hiemal rye into vernal rye using uninterrupted 24-hour light during the whole summer, see the remarkable article by Chailakhian (1933): hiemal rye, illuminated 24 hours a day at Leningrad for 64 days from the time of the appearance of its sprouts, produced culms—that is, behaved like vernal rye.

[23][Russian titles of articles have been translated and are put in square brackets. References are transliterated in the form used by the author.]

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[24]The correct term would be not iarovizatsiia, but estivalizatsiia (Latin *aestivalisatio*). L.B.

Factors Affecting the Nitrite Content of Treated Fish Fillets[1]

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ABSTRACT

There are considerable variations in the procedures used in the application of sodium nitrite as a preservative for fresh fish fillets. There is a corresponding lack of uniformity in the nitrite content of the treated fillets.

The complexity of the problem has been pointed out by showing the number and relative importance of the factors affecting the uptake of nitrite from a solution by fillets.

The suggestion is made either to abandon the use of nitrite as a preservative for fish or to standardize the procedures used in its application.

INTRODUCTION

Sodium nitrite is one of the few chemical preservatives permitted by the Department of National Health and Welfare in Canada for use with fresh fish*. The regulation states that the amount in the finished product may not exceed 200 parts per million (ppm).

If used in the very small concentrations permitted by this regulation, sodium nitrite in fish is free from harmful effects to the consumer. In considerably larger concentrations it is poisonous. About 2 g taken at one time is sufficient to kill an average man (Naidu and Venkatro, 1945). This is no reason to be fearful of the proper use of sodium nitrite. But it is an extraordinarily good reason for making sure that it be used properly. There is a margin of safety between the concentration of nitrite legally permitted in fish and the concentration that may be harmful to the consumer. Nevertheless it is important that the fish processors keep the nitrite content of fish within the legal requirements. Otherwise, they run the risk of having their products seized and destroyed.

Difficulty of Getting an even Distribution of Nitrite in Fish

With most food products the concentration of an added preservative can be controlled easily. An example of this is the addition of sodium benzoate to catsup. A measured amount of the benzoate is added to a known amount of catsup and stirred to give a uniform distribution of the required concentration.

It is not the same when sodium nitrite is added to fillets. The plant operator starts with a solution containing a measured amount of nitrite (usually between 0.2 and 0.4%). In this solution he immerses the fillets for a short period (usually between 2 seconds and 2 minutes), hoping that they will absorb enough nitrite from the solution to preserve them and hoping at the same time that the concentration will be below the maximum 200 ppm permitted by law. Unfortunately

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*Since this paper was submitted for publication, the provision of Food and Drug Regulation B.16.006 for the use of sodium nitrite in fresh fish and preserved fish in an amount not exceeding 200 parts per million of the finished product was rescinded by Order in Council of July 16, 1959, thus prohibiting the use of sodium nitrite in these items — *Editor*.

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individual fillets do not all take up the same amount of nitrite. Instead of a uniform distribution as in the case of the benzoate in the catsup, there are always differences between the nitrite contents of different fillets. The best that one can hope for is that the nitrite concentrations in a group of fillets will be within a reasonably narrow range.

It is most important to realize this fact that the nitrite in treated fillets is never uniformly distributed. As an example of this, Table I shows the nitrite content of 10 fillets that were picked indiscriminately from the packaging tables

TABLE I. Nitrite contents of treated cod and haddock fillets taken from the packaging lines of eight plants.

	Nitrite content in parts per million							
Fillet No.	Plant A	Plant B	Plant C	Plant D	Plant E	Plant F	Plant G	Plant H
1	13	80	85	107	90	88	130	163
2	16	80	87	113	110	104	149	171
3	17	86	96	116	122	120	150	178
4	17	90	104	123	126	124	153	178
5	18	95	109	126	127	136	162	182
6	18	98	109	128	128	142	170	185
7	18	107	123	132	145	172	181	188
8	19	135	128	137	149	183	181	192
9	19	140	134	141	153	190	181	197
10	23	145	143	149	166	213	186	203
Mean	17.8	106	119	127	132	147	164	184
S.D.	2.4	24	19	12	21	39	18	11
80% c.l.[2]	14–21	73–139	86–138	110–144	104–166	93–201	139–189	169–199
98% c.l.	11–25	38–174	58–166	93–161	73–191	37–257	111–215	153–215

[2]c.l. = confidence limits.

from each of 8 different plants. The foreman of each of these plants believed his fish contained approximately 200 ppm and that the nitrite content in each fillet was approximately the same. The standard deviations indicate the extent of variation of individual values around the means. The 80 and 98% confidence limits show the range of individual values that could be expected from large numbers of similar fillets that were treated in the same manner. The low values in the case of plant A show that something is obviously wrong with the dipping procedure or the concentration of the solution that was used. The variation between fillets is greatest in those from plant F, having a standard deviation of 39 and 98% confidence limits of 37 to 257 ppm.

The values shown in Table I are from groups of fillets of similar size and each fillet within the group had approximately the same history and treatment. The ranges of nitrite values are much greater when the selection is made from a greater variety in size and condition of the fish. This is indicated in Table II, which contains unpublished data obtained through the courtesy of D. C. Horne and

TABLE II. Nitrite content of large, medium, and small fillets from ten plants[a].

Plant No.	Nitrite content in parts per million		
	Small fillets	Medium fillets	Large fillets
1	45	45	31
	90	104	77
2	95	72	35
	194	200	265
3	473	412	381
	209	135	155
4	189	216	135
	243	221	134
5	286	279	238
	175	153	116
6	68	68	52
	78	72	65
7	216	95	86
	162	207	252
8	194	162	113
	99	72	72
9	189	207	144
	279	216	351
10	57	81	57
	61	48	68

[a]These figures were obtained through the courtesy of the Canada Department of Fisheries, Fish Inspection Laboratory, Halifax, N.S.

P. M. Winchester of the Canada Department of Fisheries, Fish Inspection Laboratory, Halifax. In this case two large, two medium, and two small fillets were obtained from each of 10 plants where nitrite dips were being used. It may be seen that the values range all the way from concentrations that are too small to have any preservative action to those that are considerably in excess of the value permitted by law.

Examination of results such as those given in Tables I and II suggest that there are three essential requirements in the application of nitrite to fillets: (1) to obtain a high average nitrite content, (2) to have a narrow range of values among the individual fillets, and (3) to keep within the permitted maximum of 200 ppm.

These requirements are not being attained in fish plants at the present time. The obvious reason is that the plant managers have not been informed of, or are not particularly interested in, the complexity of the problems involved. Not more than one or two plants in eastern Canada have facilities for making nitrite determinations and, so far as we know, routine checks on the nitrite content of fillets are not carried out in any plant in the Maritimes. It is also true that those persons to whom the industry looks for technical advice have not always been well informed on the subject.

To utilize nitrite intelligently, one must be familiar with the various factors that influence the amount taken up from a solution by a fillet, and understand their relative importance. The purpose of the work described here has been to study the effect of some of the more important of these factors in the commercial nitrite treatment of cod and haddock fillets.

EXPERIMENTAL METHODS

The fillets used were all obtained from a fish plant and were produced under normal commercial conditions. They were all cut from trawler-caught cod and haddock that, with stated exceptions, had been iced 2 to 6 days in stowage before landing. They were hand filleted but machine skinned. Quite often fillets skinned by machine tend to be more uneven and ragged than those skinned by hand. These fillets, therefore, were not especially good from the standpoint of their physical condition.

The sodium nitrite used in these experiments was "reagent grade" and the water used in preparing the solutions was from the Halifax City water supply. The nitrite determinations were made by the method described by Dyer (1946), using an Evelyn photoelectric colorimeter. In every instance the extract was prepared by blending the *whole* fillet with twice its weight in water using a commercial size Waring Blendor.

The general procedure has been to obtain fillets that were of approximately the same size and in the same physical condition and dip them in nitrite solutions under conditions which were made to differ by only one factor from one test to the next. The most difficult factor to control and to measure was the physical condition of the fillet (i.e., the degree of softness, broken uneven surface, and flaking apart of the muscle).

Two different methods were used for immersing the fillets in the nitrite solutions. In the first, the fillets were placed in a deep wire-screen basket which was plunged up and down in the solution. This movement caused the suspended fillets to have a slight twisting and bending motion and quite vigorously agitated the solution. In the second method the fillets were spread out on a flat wire screen which was gently immersed and slowly moved in the solution. In this case the fillets did not bend or twist and the solution itself was not so vigorously agitated. These two methods of immersion are somewhat comparable to the commercial practices of the manual dipping of fillets in wire baskets and the carrying of fillets through dipping tanks by mechanical conveyors. For the sake of convenience these methods have been termed "vigorous" and "gentle" agitation.

The proportion of fillets to solution was not always the same but was usually in the order of 1 to 10. Where deviations from this did occur, it was always with a greater proportion of dipping solution.

In most of the experiments a single test consisted of dipping 10 to 20 fillets at one time under a given set of conditions. The results have usually been recorded in terms of the average nitrite content of the treated fillets in parts per million, the standard deviation, and the 80 and 98% confidence limits for individual values.

EXPERIMENTAL RESULTS

Nitrite Concentration

Two series of tests involving the concentration of nitrite solutions were made with haddock fillets of medium size. In the first, the fillets were gently agitated for 10 seconds in solutions containing from 0.1 to 0.7% sodium nitrite. In the second, the fillets were vigorously agitated for 1 minute in 0.1 to 0.5% solutions. The

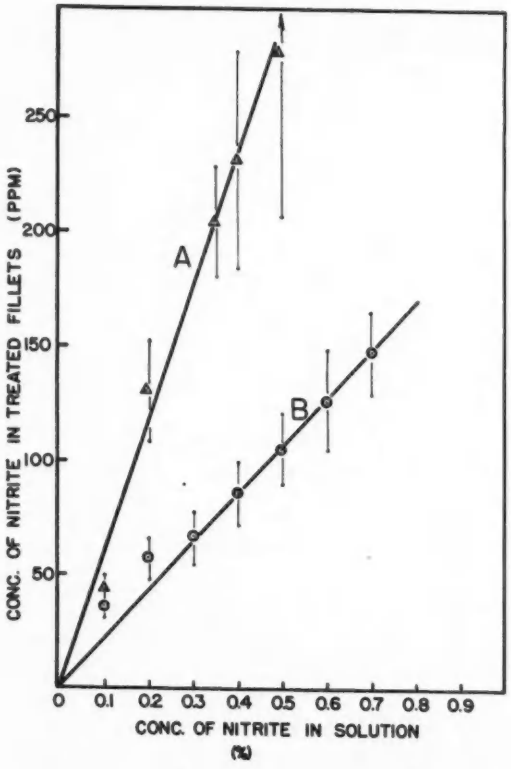

FIG. 1. Relation between the concentration of nitrite in the dipping solutions and the concentration of nitrite of treated fillets. In series A the fillets were immersed for 1 minute with vigorous agitation; in series B, for 10 seconds with gentle agitation. The vertical lines represent the 80% confidence limits.

temperature of the fillets at the time of dipping ranged between 2 and 5°C and of the solutions between 2 and 6°C. The results, as shown in Fig. 1, indicate that the uptake of nitrite by the fillets is directly proportional to the concentration in the solution.

IMMERSION PERIOD

In most modern plants where nitrite is used as a preservative the immersion periods have been reduced to 5 or 10 seconds, but sometimes individual fillets or groups of fillets may be inadvertently left in the solution for a much longer period.

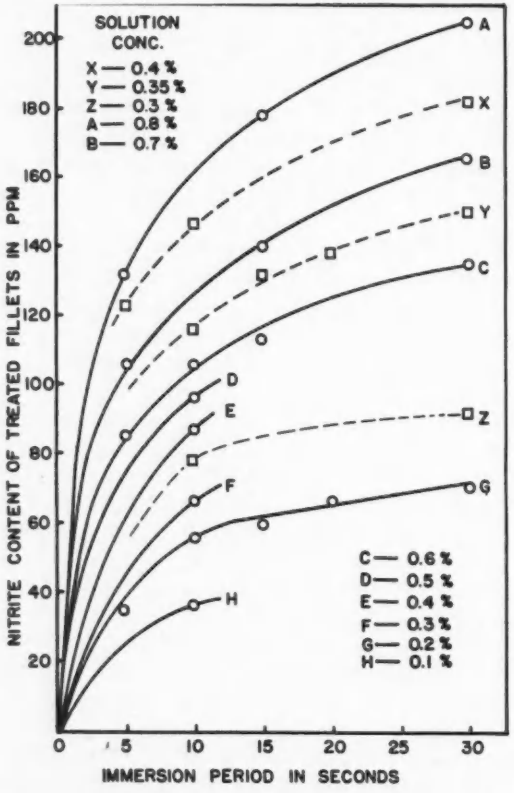

FIG. 2. Effect of immersion time on the average nitrite content of 10 treated fillets using from 0.1 to 0.8% nitrite solutions. The temperatures of the fillets were between 2 and 5° C, and those of the solutions between 4 and 5° C at the time of dipping. Curves A to H were obtained with fillets that were gently agitated during immersion; curves X, Y, Z with fillets that were more vigorously agitated.

For this reason, the experiments involving variation of the immersion periods have been carried out for two test ranges—one for 5 to 30 seconds and the second for 1 to 60 minutes. The results (Fig. 2 and 3) show that the nitrite in the treated fillets is not directly proportional to the immersion time. These curves can be

converted into straight lines by plotting logarithms of the immersion times against the nitrite values of the treated fillets.

Even though the proportion of nitrite picked up by the fillets decreases as the immersion time is increased, nevertheless it may be seen that with solution concentrations above 0.2%, illegal amounts of nitrite are easily obtained when the time is carelessly or inadvertently increased beyond the required immersion period.

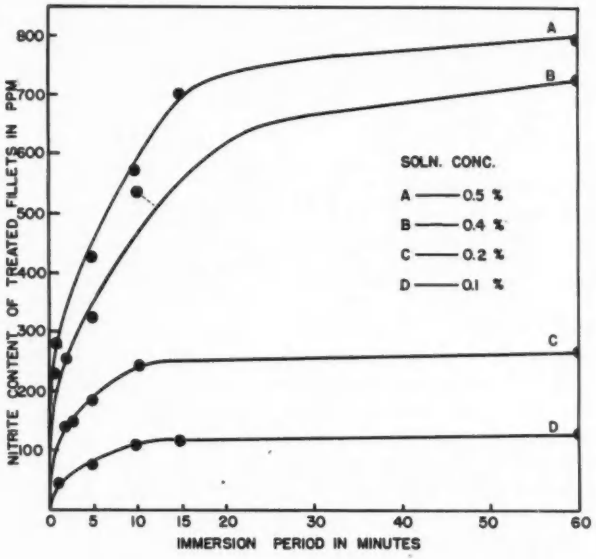

FIG. 3. Effect of immersion time on the average nitrite content of 20 treated fillets using 0.1 to 0.5% nitrite solution. The temperatures of the fillets and solutions at the time of dipping were between 2 and 5° C. The fillets were agitated vigorously during immersion except for the 60-minute immersions where the fillets were agitated at 5-minute intervals only.

TEMPERATURE OF THE SOLUTION

Large haddock fillets (380–450 g) which were at approximately 13° C (56° F) were immersed for 30 seconds in solutions that were at 0, 5, 10, and 15° C (32, 41, 50, and 59° F). It may be seen (Fig. 4) that there is a small but direct effect of the temperature of the solution on the amount of nitrite taken up by the fillets. It was also found that by holding the temperature of the solution constant and raising the temperature of the fish at the time of immersion, there was a small increase in the fillet nitrite content. For example, with solutions at 0° C (32° F) and fillets at 0, 10 and 18° C (32, 50, and 65° F) for 30-second immersion periods, the resulting nitrite contents of the fillets were 106, 129, and 135 ppm.

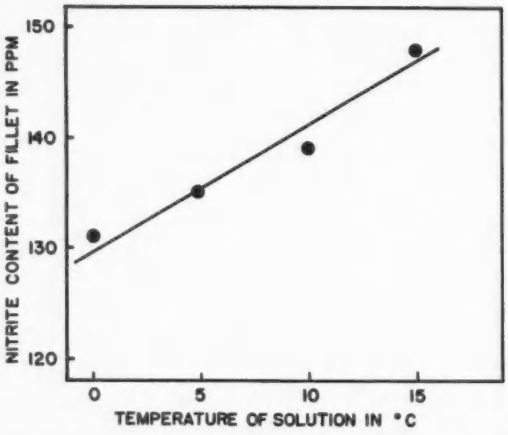

FIG. 4. Effect of temperature of the solution on the amount of nitrite taken up by large (330–450 g) haddock fillets immersed for 30 seconds with vigorous agitation.

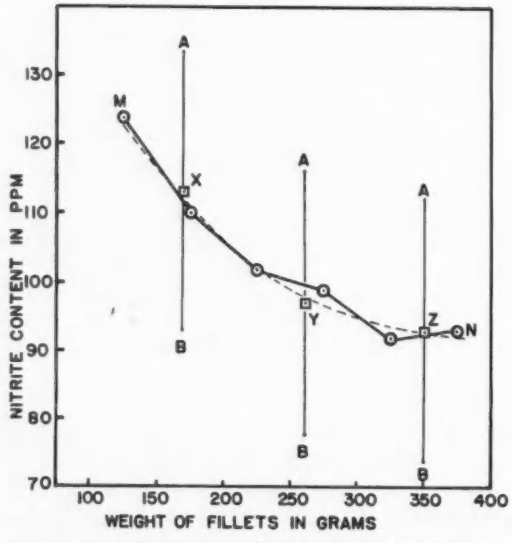

FIG. 5. Relation between size of fillets and their nitrite concentration after a 10-second dip in a 0.5% solution. X, Y, Z are mean values for small (100–200 g), medium (210–290 g), and large (300–420 g) fillets. A—B are 80% confidence limits for individual values. The values in line MN are mean nitrite concentrations of the same fish grouped in ranges having a weight-spread of 50 g.

Size of Fillets

Small fillets generally take up relatively more nitrite than larger ones but even under experimental conditions there may be considerable variation between individual fillets.

In one experiment 20 large (300–400 g), 20 medium (210–290 g), and 20 small (100–200 g) haddock fillets were immersed for 10 seconds in a 0.5% nitrite solution. In Fig. 5, the average weights of these three lots of fillets are plotted against their average nitrite content, giving the points X, Y, Z. The vertical lines A—B represent the 80% confidence limits for individual fillets in these three groups. Using the same fillets and nitrite determinations the average nitrite content of fillets in each 50-g range was also calculated. This gives the curve MN.

Physical Condition of the Fillet

As a fish becomes older (i.e., held in ice or cool storage for longer periods) the flesh becomes softer and tends to open more easily at the flakes. "Spent" fish and fish caught or held in relatively warm waters also tend to become soft. And finally, the care with which the fish is cut and skinned may make a considerable difference in its physical condition. Machine-skinned fillets are usually more ragged and more open than corresponding hand-skinned fillets. Up to the present no consideration has been given to this factor of physical condition of the fillets in the use of nitrite dips.

In the first set of tests in this series, 10 fillets cut from 8-day-old fish and 10 fillets cut from 1-day-old fish were selected so as to have approximately the same weights for each pair. These were dipped for 30 seconds in a 0.4% nitrite solution. The individual nitrite values for each fillet are given in Table III. The results are

Table III. Nitrite concentration of fillets that had been stored in ice for 8 days or for 1 day previous to being dipped for 30 seconds in a 0.4% sodium nitrite solution with vigorous agitation. Temperatures of the fillets and the solution were between 5 and 6° C (41 and 43° F) at the time of dipping. The average trimethylamine (TMA) value for the ten 8-day-old fish was 9.76 and that of the 1-day-old fish was 0.69.

8-day-old fish		1-day-old fish	
Fillet weight	Nitrite concentration	Fillet weight	Nitrite concentration
g	*ppm*	*g*	*ppm*
500	104	500	140
480	124	490	144
390	164	390	124
370	112	370	104
350	140	340	115
340	212	330	104
340	156	330	128
330	232	320	124
330	188	320	115
300	128	310	148
Average 373	156	370	125
S.D.	40.8		14.3
80% confidence limits	100–212		85–165
98% confidence limits	42–270		105–145

typical of similar tests made with other lots of fresh and spoiling fillets. The older fillets do not uniformly have higher values than the fresher ones, but they have a higher average and a much larger standard deviation. It was observed that those individual fillets with high nitrite values were softer and more broken than the others.

In a second test 40 fresh and very similar fillets were divided into four groups. The first ten were left as they were; the second ten were cut into 1-inch squares; the third ten were purposely opened at the flakes but left whole; and the fourth ten were ground in a meat grinder. Each diced or ground fillet was placed loosely in a small cheesecloth bag and treated as though it was an individual whole fillet. The resulting nitrite values (Table IV) show plainly that opening the muscle at the flakes and sub-dividing the fillets have a marked effect on the uptake of nitrite from the solution.

TABLE IV. Effect of the physical condition of four groups of 10 fillets on the nitrite concentration of treated fillets. These fillets were immersed for 30 seconds in 0.35% nitrite solution, with vigorous agitation. The temperature of the fillets was between 2 and 4° C (35 and 39° F) and that of the solution was 2.5° C (37° F) at the time of dipping.

	Normal fillets	Diced	Flakes opened	Minced
Average nitrite concentration (ppm)	148	239	259	529
Standard deviation (ppm)	17.5	14.0	23.4	80.0
80% confidence limits (ppm)	128–172	220–258	227–291	418–640
98% confidence limits (ppm)	99–197	199–278	183–325	303–755
Average weight (grams)	280	275	270	270

AGITATION OF FILLETS IN THE SOLUTION

The degree of agitation of the fillets while they are immersed in the solution also has a marked effect on the nitrite uptake by the fillets. An example of this is given in Table V. One set of fillets was gently immersed in the solution and left without further movement; two sets were gently immersed and then gently moved while in the solution; two other sets were quite vigorously agitated while in the solution. It may be seen that vigorous agitation almost doubled the nitrite uptake.

TABLE V. Relation between the degree of agitation of fillets while immersed in the dipping solution and the nitrite content of the treated fillets. The immersion period was 10 seconds and the temperatures of the fillets and the solution were between 4 and 5° C (39 and 41° F) at the time of dipping.

Agitation of fillets in the solution	Average nitrite content	Standard deviation	Confidence limits		Average fillet weight
			80%	98%	
	ppm	*ppm*	*ppm*	*ppm*	*g*
None	78	19.1	52–104	25–131	298
Gentle	86	10.3	72–100	57–115	306
Gentle	91	7.5	81–101	70–112	301
Vigorous	148	18.6	122–174	96–200	299
Vigorous	147	9.3	130–160	121–173	322

Stability of the Nitrite Solution in the Dipping Tank

Although not directly related to the thesis of this paper, from a practical standpoint it is important to know whether there is a reduction in the nitrite concentration of the dipping solution under normal working conditions.

Through the courtesy of a local plant there was an opportunity to investigate this point. In this particular plant the solutions were used continuously for 2-hr periods, and then replaced with fresh solutions. During the 2-hr periods when these observations were made, approximately 2400 lb (1100 kg) of haddock fillets were treated by means of mechanical conveyors that immersed each fillet for approximately 10 seconds.

At the beginning of one run the concentration was 0.403% and at the end of the 2-hr period it was 0.383%, which is a relative reduction of about 5%. Continuous checks on the treated fillets showed no discernible reduction in the amount of nitrite taken up by them during this 2-hr period. How much longer the solutions might have been used without a commercially appreciable change is not known, but repeated tests have confirmed that the nitrite content of the solutions used for dipping does not decrease seriously during the first 2 hours of use.

DISCUSSION

At the present time there is a decided lack of uniformity in the procedures used by different plants in treating fish with sodium nitrite. The strengths of the dipping solutions vary from 0.1 to 0.5%; the immersion periods vary from "instantaneous" to 8 minutes, and at times fish may be inadvertently left in the solution for even longer periods. The temperatures of the solutions vary from 0 to 18° C (32 to 65° F). The method of immersing the fillets in the solution varies from plant to plant.

As a result, there is a corresponding lack of uniformity in the amount of nitrite found in fish from different plants. Samplings have shown mean values ranging from near 20 to over 200 ppm. Even more disturbing is the variation frequently found in the nitrite values for individual fillets of a group that are assumed to have approximately the same nitrite content.

There are two possible steps that could be taken by those interested in improving this situation. First, a more systematic approach could be made in the application of nitrite to fish in the plants. Standard procedures with defined concentrations, immersion times, temperatures and methods of immersing the fillets could be established. Second, a more reliable system of sampling and recording the nitrite content of fillets should be developed. Average values on a few fillets have little or no meaning where plants treat millions of pounds of fish and where no consideration has been given to species, size, or to the physical condition of the fillets.

The results recorded in this paper suggest that the factors affecting the uptake of nitrite by fillets from a solution may be listed in the following order of decreasing importance:

1. The concentration of the nitrite in the dipping solution.

2. The immersion period.
3. The degree of agitation and the method used for immersing the fillets in the solution.
4. The physical condition of the fillets.
5. The size of the fillets.
6. The temperature of the fillets and the solution.

By the use of mechanical conveyors, it is possible to immerse fish in a nitrite solution for a given period under conditions that would minimize differences in the degree of agitation of the fillets when being treated. It is possible, therefore, to control the three most important factors that affect the nitrite uptake.

It is obviously impossible to avoid variations in size and in the physical condition of the fish. Compensation for these factors could most easily be made by changing the speed of the conveyor that carries the fish through the solution. In cases where plants find it useful or more convenient to treat mixed sizes of fish at one time the speed would have to be adjusted to give the correct amount of nitrite for the smallest fillets.

The control of the temperature of the solution at first appears to present considerable difficulties. Unless the solution is cooled for the purpose of chilling the fish, it is impractical to try to control its temperature by artificial refrigeration. The reason is that the temperature of the solution will to a great extent be determined by the temperature of the fish passing through it. However, in most plants where fish are stored in ice, and where there is a supply of reasonably cool water, this problem presents little difficulty. If the solution remains below 13° C (55° F) it should be quite satisfactory.

The obvious question for the plant operator to ask at this point is: "What nitrite concentration and what immersion periods will give the most satisfactory results?"

Before this can be answered we must first determine what is meant by a satisfactory nitrite content. If all the fillets are to have exactly the same nitrite content the most satisfactory value would be between 199 and 200 ppm. This would give the maximum preservative effect and still remain within the law. But, as we have seen, the fillets will not all have the same nitrite content. If we should strike an average value of 199 ppm, it means that a considerable proportion of the individual fillets would have nitrite values beyond the 200 ppm permitted by law. On the other hand, if the nitrite was lowered to the point where every fillet had less than 200 ppm, a large proportion would then have such a low nitrite content that it would be ineffective as a preservative. Somewhere a reasonable balance must be struck between the demands of the public health authorities and the requirements for effective preservation. For satisfactory preservative action the concentration of the nitrite in the fillets should not fall below 100 ppm, and a minimum of 150 ppm is preferable.

With this in mind the following standards are proposed for the permissible nitrite content in a large group of fillets: based on proper sampling, the upper value of the 80% confidence limits (and therefore also the average) must be

below 200 ppm; at the same time, the upper value of the 98% confidence limits must be below 250 ppm. In support of this, several further considerations must be pointed out. Immediately after being treated with nitrite the fresh fillets are usually packed in 5-lb or 20-lb boxes where there is some opportunity for the nitrite to diffuse from the surface of one fillet to another and thus become more uniform. Very frequently fillets are stored in ice. The melting ice water tends to leach out and therefore diminish the nitrite content. Lastly, bacterial activity gradually reduces the nitrite content of the fish.

Under the conditions existing in most plants at the present time these standards would necessitate in the fillets an average nitrite concentration somewhere between 150 and 180 ppm, which would allow for variations in the individual values.

If these recommended standards were acceptable both to industry and to those who administer the Canada Food and Drugs Act, it would then be possible to make more concrete recommendations regarding the standard procedures for dipping fillets.

Subject to modification through further study and practical experience the following procedures are recommended:

(*a*) *For fillets that are transported mechanically through the nitrite solution.* All reasonably fresh and firm cod and haddock fillets weighing more than ½ lb (225 g) should be dipped for 10 seconds in a 0.6% solution where the temperature of the solution remains below 55° F (13° C).

(*b*) *Similar fillets that are treated manually* should be placed in wire baskets or perforated containers and plunged up and down in a 0.4% solution for 20 seconds at 55° F (13° C) or below..

(*c*) *For smaller fillets and for soft or ragged fillets* the above concentrations should be reduced to 0.5 and 0.3% respectively; *or* the dipping times should be reduced to 5 seconds for the mechanical immersion and 10 seconds for the manual immersion.

(*d*) If a plant intends to treat all fillets, regardless of size and condition, in the same manner, the procedure listed in (c) should be used.

It must be pointed out emphatically that these recommendations are for exact measurements of immersion time and concentration, and that they require a constant amount of agitation of the fillets when in the solution. Ten seconds does not mean anywhere from 6 to 18 seconds!

These recommended nitrite concentrations are lower than the values indicated by the results of the tests shown in Fig. 2. It must be remembered, however, that the values shown in Fig. 2 were obtained with selected fish, treated under well controlled laboratory conditions. In commercial practice, the fillets would include a much greater variation both in size and in physical condition, which could result in higher mean values and quite probably a much larger standard deviation.

It must be pointed out further, that although these recommendations are based on the best available information, it is still the responsibility of the plant operators to see that their products remain within the limits prescribed by law. It

is important, both for their own satisfaction and for the safety of consumers to have their procedures and the nitrite content of their fillets checked by competent authorities.

Even with the greatest of care, the proper distribution of nitrite in commercial fillets will remain a problem. It is complicated by the requirements of the Food and Drugs Act and the number of factors affecting nitrite uptake. As an alternative to sodium nitrite as a fish preservative, the Food and Drugs Act permits the use of the more effective but more expensive antibiotics, chlortetracycline and oxytetracycline (CTC and OTC). It is interesting to compare the difference in the problems involved in trying to arrive at a satisfactory solution concentration for these two classes of preservatives.

In brief it is this: the law permits concentrations of the antibiotics in fish up to 5 ppm. In practice, most fillets are dipped in solutions that result in antibiotic concentrations in the fish of 0.1 to 0.5 ppm. The amount of antibiotic required for the satisfactory preservation of fresh fillets is from 1/10 to 1/50 of the maximum permitted by law. In contrast, to be very effective as a preservative, the nitrite content of the fillet must be as high as the law will permit. It is for this reason that the use of nitrite involves much more difficulty than the similar use of the antibiotics. One cannot help but wonder whether it might not be better to replace nitrite completely with antibiotics in those instances where it has been found necessary to use a preservative.

SUMMARY

It has been found that there is a wide range in the average nitrite concentrations (from 20 to over 200 ppm) of nitrite-treated cod and haddock fillets from different fresh-fish processing plants. The standard deviations in the nitrite values for individual fillets in similar groups have been found to range from 3 to 40 and are usually between 12 and 25.

The factors affecting the uptake of nitrite by fillets from a dipping solution were found to be in the following order of decreasing importance: concentration of the nitrite solution, immersion period, degree of agitation while in the solution, physical condition of the fillet, size of the fillet, and temperature of the solution.

Suggestions for standardizing the dipping procedures have been made, but it has also been pointed out that with the best of care, under commercial conditions, it is very difficult to obtain a uniform distribution of nitrite among the fillets.

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Notes

Variation in the Annual Average Weight of Chum Salmon Caught in British Columbia Waters, 1946 to 1958

The Fisheries Association of British Columbia weighing station data have been used earlier to describe annual variations in the average weights of seine-caught pink salmon in British Columbia for the period 1944–1958 (Godfrey, 1959). The same source of information is now employed to describe the yearly changes in average weights of seine-caught chum salmon (*Oncorhynchus keta*) for the years 1946 to 1958.

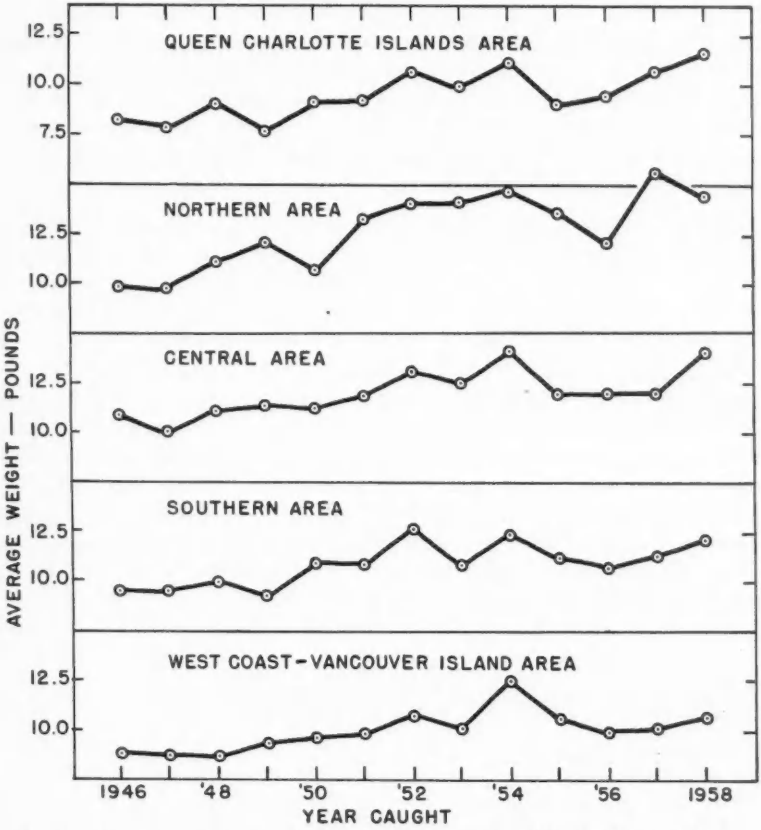

FIG. 1. Annual average weight (whole fish, not dressed) of seine-caught chum salmon in the five major Fisheries Association areas in British Columbia, 1946–1958.

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In the case of chum salmon, however, no age determinations were made, so that it has not been possible to classify these data according to age-group. Thus, because the age composition of runs of adult chum salmon can vary from year to year, some of the change in their annual average weight is due to this factor rather than wholly to actual differences in amount of growth. This may be an important source of variability, and one that cannot be corrected for in the present instance. Nevertheless, analysis of these data does indicate the following events:

(a) During 1947 to 1954 there was a general rise in the average weight of chum salmon in all five major Fisheries Association areas (Fig. 1). A sharp decline in weight occurred in 1955 and 1956, followed by an increase in the next two years (with certain exceptions, as may be noted in Fig. 1, although, because of the inadequacies of the data, these may not all be real).

The above trends are very similar to those already noted for pink salmon in the same areas, over the same period of years (Godfrey, 1959).

(b) In the case of pink salmon, the smallest annual average weight occurred in 1946. The smallest average weight of chum salmon (all ages included) was that of 1947. The difference could be due to the fact that most chum salmon mature at an age one or two years older than pink salmon. (The small size of immature coho, or "bluebacks" (*O. kisutch*), in the Strait of Georgia in 1946 was also widely noticed, according to Mr W. P. Wickett of this Station.)

The similarity in annual weight changes between the two species, and for each species between the several areas along the coast, suggests the possibility that many, or even all, of the stocks of British Columbia pink and chum salmon feed in the same general ocean area, where the effects of annual variations in environmental conditions influencing growth are widespread and similar.

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Comparison of Certain Scottish and Canadian Experiments in Respect of Grading Fish for Quality

Certain investigations into the grading of fish for quality which were carried out at the Fisheries Research Board of Canada Technological Station, Halifax, N.S., have recently been described in this Journal. They were studies of the relationship between the grades of quality given to fish such as cod and haddock and the trimethylamine content of the fish (Castell *et al.*, 1958; Hoogland, 1958; Castell and Greenough, 1958). Similar work has been previously carried out at Torry Research Station, Aberdeen (Ehrenberg and Shewan, 1955; Shewan and Ehrenberg, 1957; Reports of the Food Investigation Organisation, 1952, 1953, 1954, 1955).

In trying to compare the two sets of results from Halifax and Aberdeen, the following points emerge:

(a) From the published information on the three-point grading system used in Halifax, and also from some rather limited practical experience of this system which one of us (J.M.S.) gained during a visit to the Technological Station at Halifax in July 1957, it would appear that Canadian Grade I might correspond roughly to Raw Odour scores of 8 and above on the 10-point scoring scale used in Aberdeen, and Grade III to scores of 6 and below. This must, however, be only an extremely imprecise comparison of the two scales.

(b) Trimethylamine (TMA) was measured in Halifax as milligrams of TMA nitrogen per 100 g of muscle and in Aberdeen as milligrams of TMA nitrogen per 100 ml of muscle extract. In a statistical analysis of the Canadian data, Hoogland (1958) has also adopted a transformation of the TMA values of the form $\log_{10}(1+\text{TMA})$; the same transformation had in fact been previously developed in Aberdeen, following a detailed analysis of TMA spoilage rates and of the variations in the TMA content of different cuts of fish and of different fish (Ehrenberg and Shewan, 1955; Report of the Food Investigation Organisation, 1952, 1953, 1955).

Since the muscle of fish like cod, for example, contains about 80% moisture, our TMA measurement expressed in milligrams should tend to lie about 25% higher than the corresponding one in Halifax. But when the logarithmic scale transformation is used for these two measures, it is far more cumbersome to try and compare the results, since the relationship between the two logarithmic indices is not linear.

(c) Other divergencies in method—despite a broad agreement in the aims of the investigations in Halifax and Aberdeen—are that in Halifax the grading for quality was done mainly by various experienced fish-plant foremen and fishery officers, whilst the scoring technique in Aberdeen was applied by a laboratory

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panel which was carefully trained to be consistent. Furthermore, only in Aberdeen do factors like the catch from which the fish were taken and the length of the subsequent period of storage seem to have been taken into account, by being controlled in the experimental design and then explicitly allowed for in the analysis of the results. The period of storage is, of course, known to be of outstanding importance as an experimental factor in this kind of work, whilst the choice of a specific catch has now also been found to affect the results—see for example below.

Because of these various differences in method, there is little to be gained by attempting a detailed comparison of results. Such a comparison might well point to discrepancies between the two sets of results, but it would not be easy to establish the extent to which these discrepancies are real or are the result of methodological differences. It seems unfortunate that the experiments which were carried out in Halifax were not geared to produce results of a kind which could be compared with our earlier ones, and that it is therefore impossible to gain that broader degree of knowledge which might have come from the use of comparable techniques. No doubt there were good reasons for adopting a different methodological approach; it would be useful to workers elsewhere to learn what these were.

In conclusion, the following general remarks may be of some value here. It has now been known fairly well for some time past, quite apart from the various papers which have been cited here, that sensory assessments of quality for fish such as cod and haddock spoiling under normal conditions of storage (e.g. in ice) tend to be highly correlated with the TMA content of the fish muscle. But the more recent investigations in Aberdeen, where the unreliability of the sensory assessment technique had been largely eliminated together with other sources of experimental error, have shown that the relationship between quality and TMA differed from one catch of fish to another, even when the catches were made under very similar conditions and subsequent storage was carefully controlled. If one accepts these findings one cannot take TMA content as being a measure of quality, except perhaps in a rather rough-and-ready way. We ourselves hardly know how such differences in the relationship occur, let alone why. We see little hope that a more precise relationship between TMA and sensory assessment of quality can be established by carrying out any further experiments of the kind that were already carried out by us in Aberdeen and now also in Halifax, even when they are carefully controlled.

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Biochemical Studies on Sockeye Salmon During Spawning Migration

VIII. Androgen Content of Testes[1]

A pure race of Fraser River sockeye salmon (*Oncorhynchus nerka*) was sampled before the fish entered the river (Lummi Island, Wash, U.S.A.), at Lillooet 403 km up river in British Columbia, and at the end of a 1,135-km spawning migration (Forfar Creek, B.C.). The testes of the standard male fish weighed 56.6 g at Lummi Island, 82.0 g at Lillooet and 85.4 g at Forfar Creek (Idler and Tsuyuki, 1958). A concentrate of the testicular hormone(s) in 1 kg of testes from each location was prepared by the 70% ethanol-hexane partition procedure of Gallagher and Koch (1929).

Androgens were determined quantitatively employing the chick comb response (Jaap and Robertson, 1953). Single-comb white male Leghorns hatched on June 27 were put on experiment July 1. Testosterone propionate was made up in corn oil at concentrations of 83.9, 143.1 and 289.7 μg/ml and 0.02 ml of each solution was applied to each comb for a period of 9 days. The control chicks were treated with 0.02 ml of corn oil per day. The entire alcohol soluble testes fraction from each location was made up to 1.0 ml in corn oil and 0.02 ml applied to each comb as above. The results are shown in the accompanying table.

Bio-assay of salmon testes extracts.

Sample	No. of chicks	Body weight	Comb weight	Comb weight / Body weight
Testosterone*		*g*	*mg*	*mg/100 g*
0	9	87.0±4.2†	28.6±3	32.2
83.9	9	71.0±3.4	37.6±3	52.6
143.1	9	79.0±2.9	68.0±7	85.0
289.7	8	87.0±2.9	150.1±20	171.3
Lummi Island	5	88.0±1.8	39.0±4	44.1
Lillooet	5	90.0±2.0	52.2±4	58.0
Forfar Creek	5	95.0±3.3	61.6±4	64.5

*Micrograms of testosterone propionate per millilitre of corn oil.
†Mean ± standard error.

The testes showed testosterone propionate equivalents of 41 μg, 106 μg and 133 μg/kg for Lummi Island, Lillooet and Forfar, respectively. When the data are calculated for the standard fish, the corresponding values are 2.3 μg, 8.7 μg

[1]Part VII of this series has been submitted to the Can. J. Biochem. and Physiol.

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and 11.4 μg. Since all the salmon extracts gave a comb growth response most nearly approximating the lowest level of the testosterone standard, the increment between this standard and the control group was used in the calculations. The hexane fractions showed no activity.

A previous bio-assay (Potter and Hoar, 1954) of the androgen content of testes from spawning chum salmon (*Oncorhynchus keta*) gave a response equivalent to approximately 73 μg of testosterone propionate per kilogram of testes. The results obtained in the present study demonstrate a significant increase in the androgen content of the testes with increasing sexual maturity for the first 250 miles of the river migration ($p = .01–.05$ as obtained by the "t" test). The experiment should be repeated using 2 to 3 times the quantity of testes (*ca.* 75–100 fish) in order to determine whether the apparent increased androgen content during the final 415 miles of the river migration is significant.

The authors wish to thank Dr. J. Biely and Mrs. B. March, of the Poultry Science Dept., University of British Columbia, for conducting the bio-assay.

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Studies on the Conversion of Fish Stickwater to Solubles
IV. Effect of Enzyme Treatment on the Viscosity of Whale Solubles

When herring solubles are prepared via the acidulation process there is a marked gelling of the product beginning in the late fall and reaching a maximum in early spring. This seasonal variation in gelling of the solubles correlates with the gelatin content of the herring (McBride, MacLeod and Idler, Submitted). Recently the whaling industry has expressed concern over the high viscosity of certain whale solubles produced by an acidulation process. Whale gelatin has a higher hydroxyproline content than herring gelatin (Eastoe, 1955) and thus the viscosity reduction due to the application of heat during the processing would not be expected to be as great for whale as for herring solubles (Ward, 1954). This fact in conjunction with a high gelatin content probably explains the extremely high viscosities (Stormer Viscometer readings of 400–500 seconds) observed for certain whale solubles. The efficacy of various proteolytic enzymes in reducing the viscosity of a commercial whale solubles has been determined (Tables I and II).

TABLE I. Changes in the viscosity of whale solubles treated with commercial proteolytic enzymes at pH 3.5. Each enzyme was added at a level of 0.5% of the total solids in the solubles sample used (solids content 48%). Samples stirred continuously for the first 100 minutes. pH of solubles 3.5, temperature 25° C.

	Stormer Viscometer values*			
Time	Control	Rhozyme B-6	Papain	Takamine bromelin
0	64.6	64.6	64.3	64.4
20 min.	52.2	52.1	44.5	41.7
40 "	48.6	51.2	40.2	35.8
60 "	49.4	48.8	40.2	35.6
80 "	48.8	48.9	39.6	31.9
100 "	48.8	48.9	39.9	31.9
160 "	55.1	55.3	38.4	30.6
24 hr.	63.0	64.2	29.7	25.9
48 "	64.4	65.8	28.2	35.9
10° C	†	†	64.3	43.7

*Each value represents the number of seconds required for a paddle in the sample to make 100 revolutions when a force of 200 grams is applied.
†Gel too heavy for test.

In the first experiment (Table I) the enzyme hydrolysis was carried out at the pH (3.5) to which the whale solubles are normally lowered to prevent bacterial spoilage. In the second (Table II) the enzyme hydrolysis was carried

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out at pH 5.0. To obtain even distribution of the enzyme in the solubles the required amount of enzyme was first uniformly suspended in an aliquot of the solubles before being stirred into the sample. During the first 100 minutes of each experiment the samples were mixed by stirring. This agitation produced a lowering of the viscosity in the control sample (without added enzyme). The lowering in

TABLE II. Changes in the viscosity of whale solubles treated with commercial proteolytic enzymes at pH 5.0. Conditions as in Table I, except that pH of solubles was 5.0 and solids content 46%.

	Stormer Viscometer values*			
Time	Control	Rhozyme B-6	Papain	Takamine bromelin
0	38.7	38.6	38.6	38.7
20 min.	34.4	33.8	29.1	28.7
40 "	34.3	33.8	27.5	24.2
60 "	34.5	33.4	26.7	23.2
80 "	34.4	33.4	26.9	22.6
100 "	34.5	33.4	26.7	22.5
160 "	35.2	33.4	25.4	21.4
24 hr.	42.4	32.5	24.4	22.8
48 "	42.6	31.1	24.0	22.8
10° C.	†	156.1	35.0	34.3

*See Table I.
†Gel too heavy for test.

the control, however, was not permanent since, as soon as the stirring ceased, the viscosity values rose to their previous levels. The results with Rhozyme B-6 paralleled the control when the pH of the solubles was 3.5 (Table I), indicating that this enzyme was not effective at the low pH. Both papain and bromelin, however, produced a very satisfactory lowering of the viscosity of the solubles and the viscosity value remained low even after the product had stood without stirring for 48 hours. When the products of enzyme digestion were cooled to 10°C, they remained fluid. The viscosity values at this temperature accentuated the greater effectiveness of the bromelin in lowering viscosity.

At pH 5.0 (Table II) Rhozyme B-6 showed some activity though it was still not so effective as papain or bromelin in the process. This result with whale solubles differs from findings with herring solubles, since in the case of the latter product all three enzymes were found to be similarly effective in reducing viscosity at this pH (McBride, MacLeod and Idler, Submitted).

Herring solubles with a solids content of 46 to 48% are not considered acceptable in this area if the Stormer Viscometer reading on it exceeds 30 seconds and a very good product would have a Viscometer reading of 17 $\pm$ 3 seconds. The results of this study indicate that enzyme treatment can be used to reduce the viscosity of whale solubles to levels attainable with herring solubles. The treatment can be carried out on the final concentrated product under acidic conditions at

room temperature. Thus, neither special equipment nor special conditions are required in the process, and at the low pH that can be employed losses by bacterial spoilage are negligible.

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